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CONTENTS

THE EVOLUTIONARY SIGNIFICANCE OF HABITAT SELECTION*

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Ever since the original enunciation by Baldwin in 1896 of the theory of 'Organic Selection' the suggestion that local differences of habit may be the starting-point for the evolution of new species of animals has been from time to time put forward in various forms. Such habit 'traditions' if entirely of a phenotypic nature can of course only exist in animals in which there is some ability and opportunity for perpetuation of a particular type of behaviour or attachment to a particular environment or locality by means of associative conditioning or other type of learning.

Some years ago, Lack (1933) emphasized the phenomenon of habitat selection in birds. At that time he expressed the view that such habitat selection might have great importance in initiating the fission of a population into groups, such separation being possibly the commencement of evolutionary divergence. But recently he has (Lack, 1940) changed his opinion and now inclines to the view that geographical isolation is normally the first step in speciation. No doubt the importance of habitat selection in the evolutionary process has in the past been overemphasized, but it seems that opinion now tends to swing too far to the other extreme. Mayr, in his excellent book, *Systematics and the Origin of Species* (to which I, in common with many others, am much indebted), after some wavering, takes up a position very similar to that expressed by Lack; he concludes that in birds, at least, geographical isolation is always primary. Once this has taken place, ecological differences may follow, and then when two forms come again to overlap geographically these ecological differences may provide an isolating mechanism of fundamental importance. While this suggestion is backed by a great many examples it is nevertheless, I believe, an over-statement, even for birds, and in my opinion is certainly not in accord with much of the evidence for other animals such as insects.

To take this group first, there is considerable presumptive evidence of the isolating effect of host conditioning in parasitic insects and, in the case of plant feeders, among monophagous or oligophagous

food specialists—such conditioning established in the larval stage tending to persist in the adult (Thorpe, 1940). This field is reviewed in the references quoted, but there are a few probable examples from recent systematic work which are worth mentioning here, in that they bear rather closely on some of the problems raised by the study of birds. Petersen (1932) draws attention to the fact that certain monophagous and oligophagous genera of Microlepidoptera are very much richer in species than are the polyphagous ones, and this provides strong presumptive evidence for postulating the isolating effect of host-plant specialization. Spencer (1940) puts forward the view that in certain forms of *Drosophila virilis* and *lattivittata* that 'psychological' isolation may be primary in speciation—in which case conditioning of some kind may possibly play an important part in the early stages. Finally, as an example of habitat selection by a parasite, based not on host relations, but (as so often in birds) on some very subtle preference for certain features of the larger environment, we may cite Flanders's (1937) records of different species of the minute Chalcid *Trichogramma* specialized for arboreal, field and marsh habitats respectively. But as to the real nature and mode of origin of this particular kind of preference we as yet know nothing.

To come now to birds, Mayr (1942), in common indeed with all others who stress the importance of geographical isolation as the first step in speciation, admits that habitat selection is vital at a later stage when the two forms have come again to geographical overlap, and of the correctness of this view there is no doubt. But there is evidence for something more than this. Elton, in 1930, pointed out the significance in birds and the possible value in evolution, of what he calls the local tradition—a theory which is in essence, though in rather different form, the Baldwin theory of Organic Selection mentioned above. In this connexion the importance of the homing tendency first needs emphasis. Homing tends to limit the effective spread of many large animals. Many of them are much more localized than might at first seem to be the case. I have recently suggested (Thorpe, 1944) that the attachment to a home may be something of the nature of the very rapid and rigid type of learning which Lorenz has called imprinting, and that we may be justified in speaking in some cases of 'habitat imprinting'. Such habitat imprinting is certainly suggested by the behaviour of some of the higher Hymenoptera which carry out exploratory flights, usually known as 'locality studies'. For

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* This paper is (in essentials) a contribution made by the author to a whole-day discussion opened by Mr Lack on the subject of the 'Ecology of Closely Related Species' held by the British Ecological Society in London in February 1944. Since the first draft was written the substance of Mr Lack's contribution has been published in the *Ibis* (1944); while an interesting contribution by Cushing in the *Condor* (1944) has also appeared. References to these works have therefore been added.

instance, in the case of the wasps of the genus *Bembex*, it is suggested that the first locality study establishes the area and immediate surroundings of the newly emerged insect as 'home' for the rest of its life, and that this may be the basis of the quite extraordinary topographical conservatism persisting year after year in some of these colonies, as described by Rau (1934). There is certainly something of this kind in birds— a locality or habitat preference—as we know from the well-established tendency of migrants to return to the district where they were reared. This would tend to foster ecological specialization at an early stage; and of course when dealing with birds we must bear in mind the vital importance of territory for successful display and breeding.

Because of such considerations I feel doubtful of the justifiability of regarding birds as fundamentally different from other animals in respect of isolating mechanisms. Ecological as well as geographical factors play their part in both. Mayr and Lack seem to lay too much emphasis on *geographical* isolation. Most birds have sufficiently well-developed powers of flight to spread over whole continents and hemispheres and to overcome almost all geographical barriers if they had the urge to do so. The phenomenon is essentially similar in many other organisms, but the scale is different. The important point is the size ratio between the niche and the effective range of the individual—or to use Timofeeff-Ressovsky's phrases, between the 'territorial fragmentation' of a population and the 'range of activity' of the individuals. A particular patch of a given plant association may provide effective isolation, based on host plant preferences, for an insect, but the size of plant association which would be necessary to provide effective isolation for a bird species may be so large as to come under the term geographic. It would seem best therefore to regard geographical and topographical and ecological isolation as three different scales of spatial isolation.

Imagine now an area where two types of habitat '*a*' and '*b*' (e.g. two different vegetational types) are available in mosaic distribution and a species confined to habitat '*a*' within that area. In some exceptional circumstances of crisis, or as a result of some slight germinal change, certain individuals of the species spread into habitat '*b*' and the young reared there become imprinted, or otherwise specialized, to the new niche. If this niche provides room for expansion, the birds of the new habitat will rapidly come to fill it, during which time they will be reproductively isolated to a considerable extent from the '*a*' habitat birds. Incidentally, as Elton (1924) has suggested, during this period of expansion into a previously empty habitat the temporary relaxation of the struggle for existence coupled with preferential mating may possibly allow of the establishment of non-adaptive mutations which may still further separate the population from the parent stock. But now suppose that,

as is very likely to be the case, there is an adjacent area in which the '*b*' habitat is preponderant or general and the '*a*' habitat absent. When the '*b*' niches in the old environment are full the '*b*' adapted population may be expected to pioneer and colonize this area which was previously closed to the species because of the absence of '*a*' niches. Thus the two forms will now be partially separated geographically though with some overlap. If there is some slight geographical or topographical barrier, the isolation of the new form will be more complete, but of course the more intense the habitat selection the less vital it will be for speciation that the topographical barrier should be impassable. Similarly, the more intense the homing tendency the more effective will slight topographical and geographical barriers be in their isolating effect. Thus, habitat change may lead to topographical isolation just as topographical isolation may lead to habitat change. Finally, any genetic change tending to reinforce an existing habitat preference originally based on imprinting, or otherwise the result of experience, is likely to be fostered by natural selection in that it will increase the adaptive efficiency to the new environment. And when once a genetic difference has been established there will be a further tendency for the development of physiological isolating mechanisms, it may be as mere adaptational by-products, or more likely as a result of a special selective process for the sake of isolation and avoidance of heterosis (i.e. poor relational balance between combinations of different wild interbreeding groups) (see Dobzhansky, 1940, 1941; Sturtevant, 1938; Mather, 1943, p. 52). This idea of the necessity for avoiding heterosis can best be grasped by a careful reading of Mather's papers to which the reader is referred for further details. The problem in the past has been that while the idea that differences of this kind are of evolutionary significance has long proved attractive to various writers, it has been difficult, without invoking some form of Lamarckism, to visualize the exact mechanism whereby behavioural differences characteristic of local populations become genetically fixed. It is true that the 'Sewall Wright effect' might be operative in small populations; but recent criticism by Mather makes the probable significance of the Sewall Wright effect appear less; and in any case Wright's theory, while it might provide for random change, would not favour the genetical fixation of variation of the same kind and *in the same direction* as the pre-existing behavioural trend based on learning.

Huxley suggests (1942, p. 542), though he provides no detailed genetical model, that the organic selection principle might be expected to account for the replacement of non-heritable variations by 'mutations' and that 'where the modifications are extensive the process of their replacement by mutations may closely simulate Lamarckism'. Recent developments in genetics and in the field of animal learning make

the concept at once more probable and easier to understand.

Mather has pointed out that the kinds of character which are likely to distinguish races and species are polygenic and that any small decrease in mating freedom between two populations, whether brought about by natural obstacles or by any other cause, will be sufficient to lessen the intensity of selection for good 'relational balance' (i.e. the balance existing in an outbreeding organism between pairs of different homologous combinations). The result of this will be that when members of two such populations or strains cross, the offspring will be heterotic. Mather further brings forward evidence to show that heterotic individuals are less fit than the parental types and that the avoidance of heterosis is probably the most widespread stimulant of isolating devices. According to Mather, such a system, once started, is self-propagating and irreversible.

Now suppose for the sake of argument that the initial basis of separation is a host-plant preference on olfactory conditioning, or a 'locality imprinting' (see Thorpe, 1944) holding the animal to a restricted locality or environment, renewed afresh in each generation; and that this is strong enough and has continued long enough significantly to reduce the intensity of selection for relational balance. There will be thus a definite selective advantage for such new variants as favour more complete isolation. Now among germinal variants of equal magnitude, those which are of the same nature and direction as the phenotypic learned response already operating will be more effective in furthering isolation and will therefore be most strongly favoured by natural selection. Thus the learned or conditioned response will give momentum to and set the direction for the selective processes tending to bring about genotypic isolation. These selective processes will thus bring about the reinforcement and perhaps the eventual replacement of non-heritable modifications by genetic modifications and will thus closely simulate a Lamarckian effect. It seems probable, therefore, that habitat preference may have an influence at a very early stage, perhaps preceding topographical separation and thus helping to originate it, and at any rate proceeding hand in hand with it. As Muller (1942) has pointed out, for spatial or topographical isolation to be an effective splitting agent *alone*, it might have to be very strong, and perhaps in birds such a situation would be very unlikely to occur. 'But the topographical isolation need not be as absolute where it is combined with either acquired or genetic-ecological adaptation to different ecological conditions, as where it constitutes the only isolating factor.'

One could hardly find a better example of 'local tradition' in birds than Schiermann's (1939) account of a little colony of yellow wagtails—though there are many others which could be cited, e.g. the long-established bat-eating colony of duck-hawks described by Stager (1941) and numerous other instances of non-heritable food habits in birds collected by Cushing (1944)—altogether a by no means negligible series of examples. All the eight or nine pairs of birds in this yellow wagtail colony, contrary to the normal habits of their species, built their nests off the ground in *Artemisia* shrubs. The birds came back to the same area and continued to do this year after year until the habitat was destroyed. Of course, in the vast majority of cases such new habits, which in this case were presumably learnt and not inherited, are usually lost as quickly as they are acquired unless they have immediate survival value, and unless the territorial and breeding behaviour of the species is such that habitat selection precedes pairing so that individuals preferring the same type of habitat tend to mate. But their very existence, even if only for a short time, is, I think, an interesting fact and one which must be borne in mind. The case of the blue goose (*Chen caerulescens*) and lesser snow goose (*Chen h. hyperborea*) in America (Sutton, 1931) is another puzzling though admittedly exceptional instance. These two forms, or species as they are usually called, are remarkably similar. Southampton Island birds probably spend their entire lives together in both summer and winter ranges. Their food, call notes, behaviour, enemies and nesting habits are amazingly similar. So are their size, weight and other physical characteristics. Yet the two seem to be very largely isolated by selective mating and by reproductive habits. A certain amount of hybridization does occur and they form strong individual attachments and are monogamous. This remarkable isolation appears to be possible owing to the strong imprinting which takes place in the life of the young bird and the strong family bond which results in the families remaining together throughout nearly the whole of the year. Miller (1942) has emphasized the remarkable case of the song-sparrows *Melospiza lincolnii* and *M. melodia*. He points out that too rigid habitat selection of the instinctive type may function in a negative way in evolution by unduly limiting the exploration of the new areas and slightly different habitats by a species. In the case of these two forms, he points out that individual variations within the two species are roughly similar. Therefore, presumably similar mutations are occurring. Yet *melodia* had broken up into about 28 North American races, while *lincolnii* has only 3. The latter, apparently through habitat selection, adheres to a more sharply defined and circumscribed environment than does the other species whose selective instincts have permitted pioneering in somewhat diverse situations, thus opening up possibilities of new adaptational adjustment and colonization of new areas. The establishment of numerous geographically and ecologically isolated colonies of *lincolnii* has been thwarted by rigid preference for a certain type of fresh-water

marsh. The positive action of habitat selection works by providing isolation of populations within a species. If pioneering of detached areas takes place, habitat selection may often help to inhibit indiscriminate dispersal of the pioneer population and hence the swamping of differences arising from isolation. Or it may itself change, so that different features of habitat are preferred and a population of a new geographical area or ecological situation is thereby held apart. Subspeciation in the song-sparrows, then, suggests, the co-operation of both habitat selection and geographical separation from a very early stage. Either factor seems inadequate alone.

Similarly the isolation of races of bird species *within* the forest belt of New Guinea mountains (Rand, 1936) seems to suggest the same thing. Again, Miller (1942), referring to the Marin chickadee, *Penthestes rufescens neglectus*, a form of the chestnut-backed chickadee, *P. rufescens*, confined to Marin Co., California, suggests that this race has perhaps been held in isolation and their distinctions promoted and preserved by habitat selection; the birds having the ability to fly across the Golden Gate but not the desire.

In conclusion, then, I think we must keep an open mind as to the part played in evolution by habitat preference—whether learned or instinctive, or both, one reinforcing the other. Birds tend to be strongly territorial animals and the claim that geographical isolation *always* precedes other kinds of isolation seems premature.

SUMMARY

1. A number of recently investigated cases of habitat selection in birds and insects are described and their possible evolutionary significance discussed.

2. It is suggested that geographical, topographical and ecological isolation are best regarded as different scales of spatial isolation.

3. It is argued that recent work on polygenic inheritance and the importance of avoiding heterosis has made the evolutionary function of learned habitat preferences in giving rise to isolating mechanisms more probable than hitherto.

4. Recent developments in the field of animal learning, particularly imprinting, suggest that such habitat preferences play their part in birds as well as in other groups such as insects. While geographical isolation undoubtedly plays a very large part in the initial stage of bird speciation, the grounds do not appear sufficient to support Mayr's claim that it *always* precedes other kinds of isolation. More probably habitat or locality preference and 'geographical' separation work together as isolating mechanisms from the start while in certain exceptional cases the former may alone initiate the process of separation.

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SLUGS IN GARDENS: THEIR NUMBERS, ACTIVITIES AND DISTRIBUTION. PART 2*.

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(With Plates 3–5 and 11 Figures in the Text)

CONTENTS

8. FEEDING HABITS

Although the feeding habits of slugs have not received particular attention by the authors, there has been ample opportunity, especially while collecting at night, to acquire some definite information concerning their customary habits in this direction. The mere mention of one or more species feeding on a particular plant or substance is not meant to convey the impression that other species do not have the same habit; it simply indicates that the species mentioned caught the eye.

The most striking feature has been the apparently infinite variety of food which seems to appeal to their taste. This being so, it seems remarkable that almost any edible bait which may be placed in a garden will attract slugs: one would have thought that they would not have bothered to go towards it, there being so much alternative food all around. But they do.

Another point is that most species and individuals normally feed at or near the surface of the ground. This accounts for the fact that the lower leaves of such plants as cabbages, leeks, onions and so on which frequently touch the ground are more often damaged than the hearts and other portions farther from the soil. One species however, i.e. *Agriolimax reticulatus*, is prone to feed higher up on plants and there are also species which feed underground, e.g. *Milax gracilis* on potato tubers; but even in this species large numbers of individuals feed on the surface of the ground.

Healthy living plants: leaves. Naturally on some occasions slugs have been found after dark in the act

* Continued from this *Journal*, vol. 13, pp. 140–75.

of eating the leaves of living healthy plants. For example, *Arion hortensis* has been seen eating young leaves of primulas during the winter and spring months, particularly when they are under a covering of fallen leaves. Large *Arion ater* have been observed eating coarse grass, and their yellow-coloured young have seemed to be partial to brassicas, campanulas and saxifrage during the early part of the year. Likewise *Arion subfuscus* has been seen eating lettuce, cabbage and campanula leaves. *Agriolimax reticulatus* has been found eating the leaves of many plants including grass, lettuce, cabbage, winter greens, scarlet runner bean, Michaelmas daisy, potato, etc.

Healthy living plants: crowns, rhizomes and tubers. Slugs are by their low feeding habits particularly fond of feeding on the crowns of plants, e.g. *Arion hortensis* on the crowns of primulas. Tubers and rhizomes of plants are also frequently attacked. Thus *Milax gracilis*, *M. sowerbyi* and *Agriolimax reticulatus* have been observed feeding on the tubers of potato and rhizomes of Jerusalem artichoke, particularly when the tubers have been left exposed on the surface of the ground.

The authors consider that *reticulatus* is not a primary pest of potato tubers and does not often start an attack on them. It is, however, a severe secondary pest and is quick to follow, and greatly increase, initial damage done to tubers by other pests, including the slugs *Arion hortensis* and the *Milax* species. Evidence supporting this opinion was obtained by keeping *reticulatus* provided with undamaged potato tubers. After several nights the

tubers were still undamaged. On the other hand, when slices of potato or tubers with slug holes in them were given to *reticulatus*, there were obvious traces where the slugs had been feeding after only one night. *Milax gracilis* and *sowerbyi*, on the other hand, bored into potato tubers the first night. In the presence of puff-balls, however, *M. sowerbyi* did not attack the potato tubers but preferred the fungi. It is desirable that more critical experiments be carried out before dismissing *reticulatus* as a primary pest of tubers. In any case, it is a very serious secondary one.

Healthy living plants: fruit. As is well known *reticulatus* loves a ripe strawberry. Luckily, with this exception, most fruits are higher from the soil and so out of the reach of slugs. Unfertilized fruit of vegetable marrow has also been seen to attract slugs of various species.

Fungi, algae, lichens and mosses. Among the larger fungi, the puff-ball must have, during part of the summer, formed a favourite item of the diet of the slugs, to judge from the numbers of *Limax maximus*, *Arion hortensis*, *A. subfuscus*, *Milax gracilis* and *M. sowerbyi* seen feeding upon groups of immature specimens. Toadstools of various kinds have also been observed to be eaten by slugs during the early autumn.

In the autumn and winter large numbers of slugs, especially very small specimens of *hortensis* and *subfuscus*, have been observed feeding assiduously on the bark of fallen twigs and larger felled branches which have been laid on the ground. It is presumed the slugs were feeding on the smaller fungi, algae, lichens and mosses which were growing on this bark.

Plant material which has fallen from plants and trees. Throughout the different seasons of the year, various plant material drops to the ground from plants and trees. Thus catkins fall in the spring. Slugs of most species have been seen feeding on walnut catkins and the male catkins of golden willow (*Salix alba* var. *vitellina*). A little later various petals fall. Again slugs have been found apparently feeding greedily on fallen petals and flowers of red chestnut, apple and pear. Still later, fruit in all stages of growth falls at intervals to the ground. Such fallen fruitlets and fruit whether sound or in different stages of over-ripeness and decay, as well as diseased fruits, seem equally attractive to many slugs. Hawthorn fruit, pears, apples and plums have all been noticed in this category. Lastly, in the autumn the fallen leaves of deciduous trees and shrubs provide a rich provender for slugs of all kinds, as well as good shelter.

All such material sooner or later develops fungi and algae on it as decay sets in, but the slugs do not wait for this to happen before starting their meals.

In addition, numerous slugs have been found devouring lawn cuttings on surrounding paths, and there have always been increased numbers of slugs found on any lawn the night after it has been cut compared with those seen on other nights.

Dying, rotting and diseased vegetable matter. One of the most noticeable facts about the feeding habits of slugs is their apparent preference for damaged vegetable matter rather than healthy plant tissues. Far more slugs have been seen feeding on wilting, drooping and wind-torn and otherwise slightly damaged leaves than on really healthy ones. This has been particularly noticeable with regard to onion, leek, daffodil and *Brassica* leaves. This may be partly due to the low feeding habits of slugs, but, even in the case of *Agriolimax reticulatus* which feeds higher up on plants, it is very noticeable how it picks out the withering and dying blossom and leaves of such plants as sweet pea and scarlet runner bean in preference to the healthy flowers and leaves. This is particularly so in the autumn. Also more slugs have been seen feeding on rotting vegetable marrows than on healthy ones. *Arion ater* seems very fond of rotting marrow.

Lastly in this section, at all seasons of the year the rotting vegetation or garden rubbish heaps, and old *Brassica* stems left lying on the ground, have been a great source of food supply in addition to being good shelter. All the slugs sheltering in such heaps do not spread out every night from them to nearby growing vegetation; many individuals have stayed on the heaps all night apparently finding plenty of food.

In drier weather, however, more slugs seem to disperse from garden rubbish heaps so long as the neighbouring soil is sufficiently moist to allow movement. *Milax sowerbyi* appears to linger longer and be less ready to move away from the heaps. It seems that this species is content to feed on much more dry material than, for example, *Agriolimax reticulatus*. Slugs also tend to leave the rubbish heaps more freely as the material forming the heaps rots down.

Flesh. *Milax gracilis* has frequently been observed eating the remains of squashed slugs of its own and other species. On one occasion it fed in some numbers on some slugs that had been killed by metaldehyde bran baits the previous night. The results were fatal.

Faeces. Another striking feature of the feeding habits of slugs in gardens has been the extent to which they are attracted to and feed on faeces. Several species, especially *Arion subfuscus*, *Milax gracilis*, *M. sowerbyi* and to a less extent *Arion hortensis*, and many individuals have been observed feeding on dog faeces in the various gardens visited. Similarly, slugs have been seen feeding on the faeces of cats, rabbits and hedgehogs.

Bones. The same species, which are especially attracted to faeces, i.e. *Arion subfuscus*, *Milax gracilis*, *M. sowerbyi* and to a less extent *Arion hortensis*, are attracted to and feed on meat and fish bones which have been given to dogs and cats respectively. This habit, together with the scatophagous one just mentioned, led us to experiment with meat and bone meal

as a slug attractant. The result was that this meal proved to be a significantly better attractant than bran for *gracilis*.

Miscellaneous substances. Miscellaneous substances on which numerous slugs have been observed feeding in gardens after dark include the following: damson and other plum stones thrown out after jam making; apple, vegetable marrow and potato peelings; porridge which had been thrown out because the milk used in making it had curdled; and dog biscuits.

Other miscellaneous substances have been used in bait trials. Those to which slugs have been readily attracted, and observed feeding upon, include bread, flour, ground rice, Quaker oats, cattle cake, cotton cake, linseed cake, middlings, yellow maize meal, castor meal, biscuit meal and, of course, bran. Other substances have also acted as attractants and possibly have provided nourishment to some extent. Among these may be enumerated sugar-beet pulp, used tea leaves and coffee grounds.

Conclusions. These observations amply prove the varied taste of slugs and that it includes healthy and decaying vegetation, plant products uncooked and cooked, cooked and uncooked meat and bones, as well as animal faeces. In an average garden which is not too scrupulously tidy and well cultivated the vast bulk of the slugs' food consists of material that would not be used for human consumption or pleasure. This explains why, although slugs are so numerous in gardens, only on comparatively few occasions are they accused of being, and are in fact, serious pests.*

9. MATING TIME AND BREEDING SEASON

Out of 34,956 slugs belonging to nine species observed and collected after dark in gardens and other places during 1942, only 288 belonging to four species were found in congress. On no occasion were specimens of *Arion ater*, *A. circumscriptus*, *Milax sowerbyi*, *Limax maximus* and *L. flavus* seen mating. These account for 2515 out of the total of 34,956. Of the remaining four species which were on occasion found mating, only 16 out of 12,010 *Arion hortensis* and two out of 6613 *Milax gracilis* were in congress. On the other hand, 50 out of 3590 *Arion subfuscus* and 220 out of 10,228 *Agriolimax reticulatus* were found mating.

In 1943 mating was observed to much the same

* It may be mentioned incidentally that *Agriolimax reticulatus* has formed the only food of a slow-worm (*Anguis fragilis*), which has been kept in captivity, from May 1942 to September 1943. This animal seems to have been adequately fed, having sloughed its skin twice between May and October (1942) and it survived the following winter. No food was given it between the end of November and mid-March. Since September 1943 up to the end of March 1944 *Arion hortensis* has formed the main diet of the slow-worm with apparently no ill effects.

extent, only 262 slugs belonging to four species, out of the total of 38,416 belonging to nine species, being seen in congress. Again *reticulatus* was observed mating most frequently followed by *subfuscus* and then by *hortensis* a long way behind. But no *gracilis* were found mating, whereas four out of 967 *ater* were.

At first sight these data seem too scanty to draw any conclusions, but further thought shows that they are not in reality so poor. It must be remembered that the duration of the collecting was only a fraction of the hours of darkness. Taking this point into consideration, as well as the fact that the method of collecting precluded all searching under leaves, etc., a most natural place for congress to take place in, the apparently scanty data seem sufficient to draw at least tentative deductions concerning the mating time and breeding season.

Tables 13 and 14 give the numbers and proportions of slugs seen mating after dark in the open during

Table 13. *Number of slugs seen mating in the open after dark, 1942*

	Arion hortensis	Arion subfuscus	Milax gracilis	Agriolimax reticulatus
Jan.	0/ 197	0/ 80	0/ 89	0/ 193
Feb.	—	—	—	—
Mar.	0/ 1,000	0/ 156	2/ 547	2/ 825
Apr.	0/ 1,157	0/ 370	0/ 283	18/ 1,190
May	0/ 580	0/ 343	0/ 727	14/ 565
June	0/ 55	0/ 254	0/ 129	4/ 264
July	0/ 215	10/ 531	0/ 302	14/ 751
Aug.	0/ 846	24/ 672	0/ 617	12/ 1,685
Sept.	0/ 1,215	12/ 325	0/ 866	56/ 1,487
Oct.	8/ 1,936	4/ 344	0/1,045	62/ 1,659
Nov.	2/ 1,778	0/ 195	0/ 726	4/ 701
Dec.	6/ 3,031	0/ 320	0/1,282	34/ 908
Total	16/12,010	50/3,590	2/6,613	220/10,228

1942 and 1943 respectively. The numbers seen mating do not bear a constant relationship to the total numbers seen or collected.

It can be seen that comparatively few *Arion hortensis* mate out in the open during the hours of darkness. From the appearance of young specimens in samples taken at all periods of the year, it would appear that breeding occurs all the year round. But it is probable that most mating and breeding takes place in the autumn and winter months. It is possible that the actual peak of mating in 1942 was in the month of October when two out of every 484 slugs seen were in congress.

It would appear that *Arion subfuscus* mates freely out in the open after dark during the four months July–October. In these months during 1942 two in every 75 were found in congress and none out of 1718 during the rest of the year. The peak of mating apparently was in August and September when two out of every 56 and 54 respectively were in congress. In 1943 two in every 58 were found mating in July–September and none out of 3676 during the rest of

the year. The peak was in August and September when two out of every 32 and 46 respectively were found in congress. Baby specimens of this species have been most abundant during December–February, while comparatively few have been encountered in the summer months. It seems likely therefore that breeding is much more restricted in this species than in *Arion hortensis*.

Agriolimax reticulatus mates still more freely out in the open after dark. Mating time in this species has been observed taking place every month of the year. Young have also been observed throughout the year. But still there seems to be a definite peak in the mating season. Thus, during 1942 in September two in every 53 and in October two in every 54 found after dark were in congress. In 1943 the most favoured months were August and October, during each of which months two in every 42 individuals found were mating. It is thought that December

Table 14. *Number of slugs seen mating in the open after dark, 1943*

	Arion ater	Arion hortensis	Arion subfuscus	Agriolimax reticulatus
Jan.	0/155	2/ 1,711	0/ 349	4/ 666
Feb.	0/ 37	0/ 781	0/ 186	2/ 355
Mar.	0/ 80	0/ 721	0/ 198	10/ 307
Apr.	0/120	4/ 955	0/ 433	12/ 356
May	0/203	0/ 1,388	0/1,323	22/ 931
June	0/144	0/ 277	0/ 869	2/1,873
July	2/ 70	0/ 201	8/ 516	22/1,092
Aug.	2/ 37	0/ 385	18/ 294	42/ 880
Sept.	0/ 23	4/ 1,042	8/ 183	18/ 787
Oct.	0/ 40	0/ 2,692	0/ 173	68/1,445
Nov.	0/ 29	0/ 809	0/ 79	12/ 317
Dec.	0/ 29	0/ 332	0/ 66	0/ 126
Total	4/967	10/11,294	34/4,669	214/9,135

1942 when two in every 53 were mating was rather exceptional, and that it is not the rule for the peak of mating to take place in this month. It would appear that conditions favouring the congress of *reticulatus* occur all the year round and that in September and October these conditions occur more frequently than at other times of the year or, another explanation, that there is a rhythm by means of which most of the slugs reach maturity in these two months.

Arion ater has only been seen mating twice, once in July and once in August, both during 1943. It is probable that this species does not usually mate in the open after dark. The breeding season is clearly shown, by the appearance of the young, to be in the autumn and winter.

The only other species of slug found in congress after dark in the open has been *Milax gracilis*. Only one pair has been observed mating (17 March 1942) under these circumstances. It is considered that it is not the rule for this species to mate out in the open or after dark. Actually two other pairs have been

found in congress, one under leaves and the other under a tarpaulin, on each occasion at 13.30 hr. (i.e. in daytime) on 7 and 11 November 1942. It should be mentioned that extremely few searches have been made during daytime, and that those that have been made have been more in the nature of glances rather than systematic searchings.

Similarly, *Milax sowerbyi* has never been seen in congress out in the field. But congress has been observed three times, all in October 1942; twice in Petri dishes on the laboratory bench, after samples collected after dark had been separated into their component species, and once in the insectary where the slugs were being kept in flower-pot saucers covered with other saucers. Congress on each occasion was taking place in daytime and was of several hours' duration. In one case it had started by 8.00 hr. and was still continuing at 17.00 hr. One pair which had mated on 1 October was in congress again on 27 October.

It would appear from these few observations that these two *Milax* species do not mate out in the open at night, but may do in the daytime under cover. It is possible that October is the peak month for *sowerbyi* and November for *gracilis*.

From what few data are available concerning mating, it would seem that the peak periods of mating in slugs are closely linked up with those of activity, which are themselves closely connected with the periods during which the slugs are largest. These points will be discussed in the next section.

10. WEIGHTS

(a) Weights in relation to amount of food eaten

The only available data of the amount of food eaten by slugs were derived from a small potato patch (10 × 10 yd.). Observations showed that the entire crop had been destroyed, literally only potato skins remaining. The coring method of sampling showed that the absolute population was in the neighbourhood of 60 per sq.yd. (or 300,000 per acre) and that 70 % of the population was *Milax gracilis*.

In order to get information on the weights of slugs, a series of weighings was made in November and December 1942 by the following method. All the specimens of any one species collected in a single sample were weighed together and the weight per 100 calculated. The slugs as usual were kept overnight in an hermetically sealed tin and they were weighed the next morning immediately after the sample had been sorted into its component species. It was found that at this season of the year the mean weight of 100 *Arion hortensis* was 21 g., of 100 *Agriolimax reticulatus* 40 g. and of 100 *Milax gracilis* 43 g.

It is obvious that the slug population on the potato patch consumed almost the entire potato crop, which could hardly have been less than 5 tons per acre.

Using the weight of *gracilis* given above, it appears that each slug ate approximately 30–40 times its own weight. The estimate of 300,000 slugs per acre is probably too low for this patch, since this figure would indicate a population of only 6200 slugs (or about 5–6 lb. weight) on the 100 sq.yd. studied, and in two months at least 2000 slugs were removed from it without apparently decreasing the population. If the population was higher, as seems likely, this estimate of total food consumed by each slug would be too high.

A mixed sample of several species of slugs from a garden in mid-November indicated that 10,000 specimens weighed approximately 6 lb., and it has just been shown that *gracilis* weighs approximately 1 lb. per 1000. From such figures it is easy to appreciate that the weight of slugs per acre may be in the neighbourhood of 180–300 lb. and that the weight of food consumed per year must be considerable. The manurial value of an equivalent weight of livestock per acre is appreciable but the value of slugs' faeces as fertilizer is not known, neither have the proportions of their different types of food been ascertained quantitatively. Furthermore, the value of aeration of the soil by slugs is not known.

(b) Weights throughout the year

It was realized that to obtain any really useful data regarding the weights of slugs, weighings would have to be made at all seasons of the year. At the same time the weights of slugs in some gardens might be different from those of slugs in other gardens. If such series of weights were obtained, information would in all probability be gained regarding the growth rate, as well as the proportion of young to old, of the various species.

Table 15. *Calculated weights per 100 individuals, April 1943–January 1944 in all gardens*

Species	Numbers weighed	No. of weighings	Range in wt. (g.)	Mean wt. (g.)
Arion hortensis	9291	117	6–.40	19
Agriolimax reticulatus	8126	152	10–86	33
Milax gracilis	9102	107	14–95	32
Arion subfuscus	3960	106	17–258	99
Milax sowerbyi	2105	103	56–269	122

Therefore starting in April 1943 systematic weighings have been made of nearly all the samples taken in the course of the activity study (Table 15). It will be seen that *hortensis* is the lightest slug, followed by *reticulatus* or *gracilis*, then by *subfuscus* with *sowerbyi* the heaviest of the five species. This corresponds with their order in size (see Part 1, § 2).

In addition to these species, the weights of *Arion ater, Limax maximus*, and *Arion circumscriptus* were noted less regularly. On only two occasions (both

in May), the last-named species was weighed. The weight per 100 worked out at 29 and 57 g. based on 17 and 7 individuals. In the case of *ater* 659 individuals were weighed, the largest weighing 21 g. (This species has been recorded elsewhere as reaching a weight of over 34 g.) In the case of *maximus* 83 individuals were weighed, the largest in this species weighing 20 g. *Maximus* appears to be biggest in May–July, whereas *ater* reaches its largest size in August–September and *circumscriptus* during the winter months.

It has been shown earlier in this paper and elsewhere (Barnes, 1944) that the behaviour of slugs as regards the general trends of activity after dark, as indicated by the method of sampling used by the authors, is practically the same whether the samples are taken in one garden frequently or one garden once in a month. The same trends of seasonal activity are observable in all Harpenden gardens visited whether the species is particularly numerous or otherwise.

Fig. 19 shows that the same general seasonal trend in weight of *Agriolimax reticulatus* is obtained whether one weighs samples collected infrequently in single gardens or frequently in one garden or at irregular intervals in many gardens. The data for the weights of slugs in the back garden of No. 5 are given in Table 16. The full data, which are voluminous and of which copies are kept in both the Entomology and Statistical Departments at Rothamsted Experimental Station, demonstrate that the same is true for *Arion hortensis* and *subfuscus*, *Milax gracilis* and *sowerbyi*. In other words, the method for obtaining the seasonal trends in weight of the different species is just as reliable as the one adopted in Part 1 for discovering the seasonal trends in numbers active. But just as the peaks of activity are higher and at slightly different times in some gardens, so in some gardens the slugs are usually heavier than in others.

The population of *reticulatus* is lightest in June and increases in weight steadily until the autumn and apparently is heaviest in April (Fig. 19). Fig. 20 shows the seasonal weights of four other species. *Arion hortensis* reaches its lowest weight during June and July and increases steadily during the autumn. The curve of *Milax gracilis* is very similar. Samples of these two species and *Agriolimax reticulatus* (Fig. 19) usually contain small and large specimens at whatever season of the year they are taken. The curve of weights of *Arion subfuscus* is different. In this case, the weights are lowest in the spring and autumn and rise steadily from April to a maximum in August. The subsequent fall in weight is equally pronounced. The curve for *Milax sowerbyi* shows a marked increase in weight during May and early June, but then the weights decrease suddenly and in late June, July and early August they reach their minima. But in the autumn the main increase in weight is apparent. By observation, the largest *sub-*
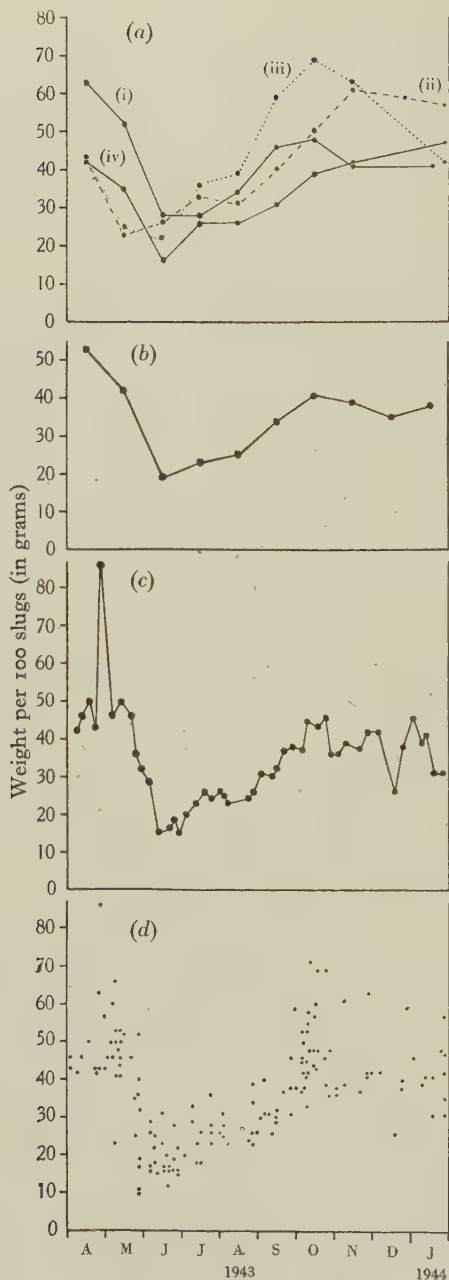
Fig. 19. The seasonal weight of *Agriolimax reticulatus*
(*a*) in the back gardens of (i) No. 10 Douglas Road,
(ii) No. 15, (iii) No. 11 and (iv) No. 7 Moreton End
Lane; (*b*) the monthly average in the back garden of
No. 5 Moreton End Lane; (*c*) per sample in the same
garden; (*d*) scatter diagram of the weights per sample
in all gardens. The weights are expressed as the weight
in grams per 100 individuals.

Table 16. *The weights in grams per 100 individuals,
April 1943–January 1944, No. 5 Moreton End Lane
back garden*

(The numbers of slugs from which the weights are
derived are to be found in Appendix 1.)

	Arion hor-tensis	Arion sub-fuscus	Milax gracilis	Milax sowerbyi	Agrio-limax reticu-latus
1943					
9 Apr.	17	30	27	71	42
13	14	26	29	80	46
18	18	43	29	—	50
23	16	70	32	75	43
27	14	53	27	91	86
5 May	13	51	30	75	46
13	18	67	28	93	50
22	14	70	27	144	46
26	14	79	26	120	36
30	10	63	26	138	32
5 June	13	73	26	125	29
13	14	73	24	93	15
21	—	87	24	67	16
24	—	94	22	—	19
28	—	82	20	—	15
3 July	—	124	23	—	20
11	—	138	29	—	23
16	—	128	19	—	26
24	11	123	22	76	23
1 Aug.	9	122	23	—	26
4	12	143	17	67	25
7	14	159	20	71	23
26	11	132	20	88	24
28	12	135	28	135	26
4 Sept.	12	111	22	94	31
10	13	132	24	126	30
16	14	119	28	137	32
21	15	111	30	185	37
28	16	119	31	164	38
5 Oct.	16	53	32	172	37
10	26	56	32	165	45
10	18	111	32	200	33
17	20	—	33	164	43
23	21	80	39	181	46
28	22	38	40	160	36
2 Nov.	24	71	40	200	36
10	20	58	31	150	39
21	21	36	32	200	37
28	20	56	32	167	42
7 Dec.	21	17	34	—	42
18	22	38	36	—	26
25	23	39	38	150	38
1944					
3 Jan.	22	21	33	175	46
9	26	33	39	100	39
12	25	29	34	100	41
18	26	25	39	133	31
26	26	32	35	—	31

fuscus slugs occur in the middle of the summer when few small ones are visibly active. Similarly, of the *sowerbyi* collected during May 1943 most were noticed to be a fair size, but then young ones started appearing and the large ones disappeared. In the autumn the majority were seen to be large, and although young ones were also present, especially in the weighing of slugs individually, are in progress in order to establish more exactly the relation of weight to numbers active.

(d) Weights in relation to the mating season

It has already been shown that the different species have different mating habits and consequently after
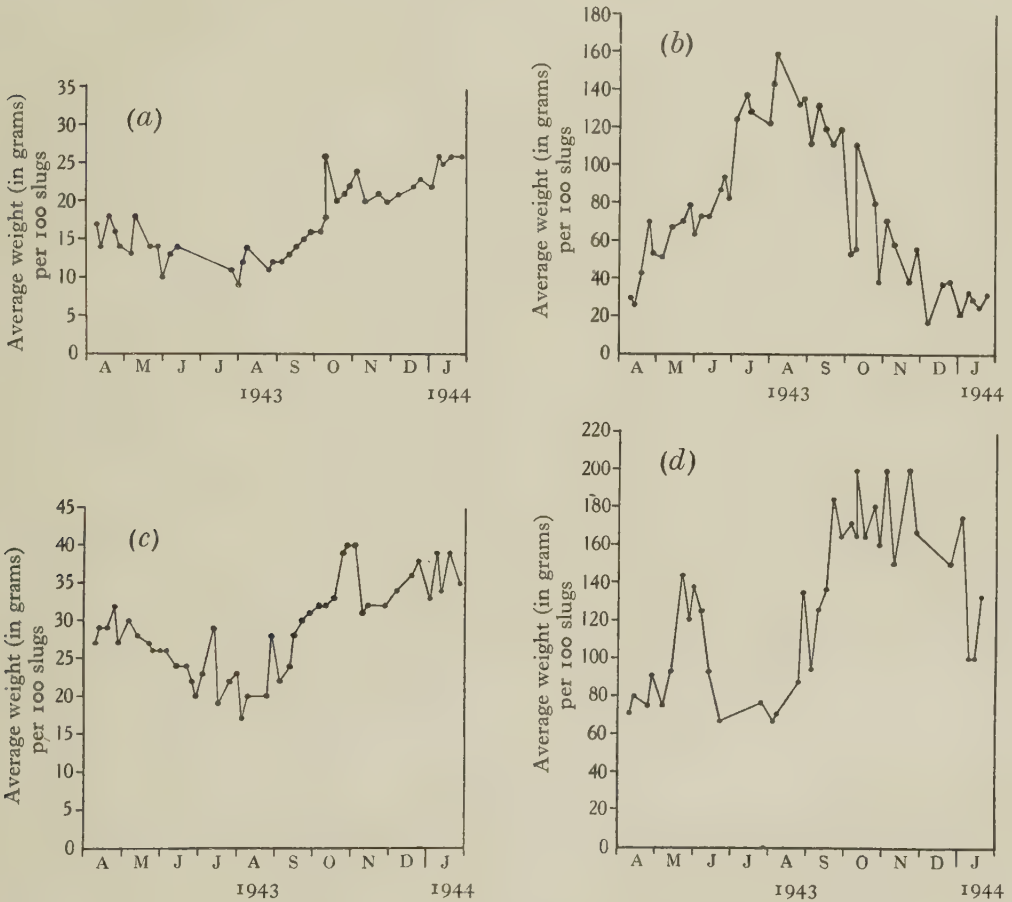
Fig. 20. The seasonal weight of (*a*) *Arion hortensis*, (*b*) *Arion subfuscus*, (*c*) *Milax gracilis* and (*d*) *Milax sowerbyi* in the back garden of No. 5 Moreton End Lane.

the later autumn months, they were always outnumbered by the large individuals.

(c) Weights in relation to seasonal activity

Fig. 21 shows the monthly average weights of five species in relation to the monthly average numbers found active after dark. The data refer in each case to the back garden of No. 5 Moreton End Lane. As a rule the slugs are heaviest soon after the greatest numbers are found active. In other words, increased numbers active usually foretell an increase in the average weight of slugs. Further investigations, involving

dark the collection of slugs visible out in the open only yields mating data for *Agriolimax reticulatus*, *Arion subfuscus* and, to a much less extent, *A. hortensis*.

Fig. 22 shows the monthly average activity and weight as well as the total number seen mating, of *Arion subfuscus* and *Agriolimax reticulatus* in all gardens visited. The peak of numbers active in *reticulatus* and *subfuscus* is quickly followed by the peak in numbers found mating, and this occurs when the slugs are heaviest. The peaks of mating in 1942 and 1943 were in the same months, whereas the

peaks of activity were slightly earlier in 1942 than in 1943. This regularity in mating season would be expected, as mating is a biological function of the

From these figures, the height of mating is not followed quickly by a relatively large increase in the numbers found active, i.e. the resulting young.
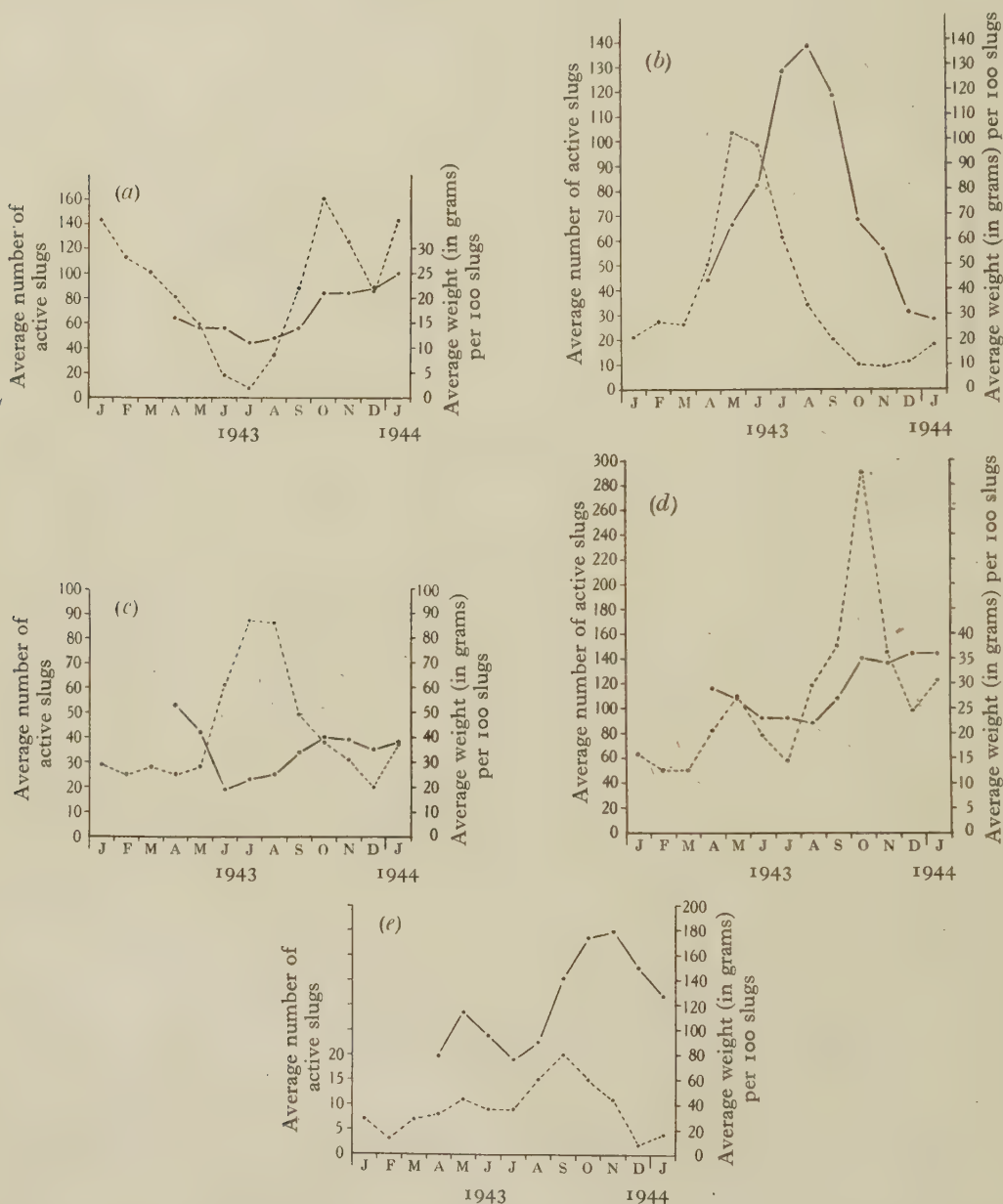
Fig. 21. The monthly average weight (——) in relation to the monthly average numbers found active after dark (----) in the back garden of No. 5 Moreton End Lane. (a) *Arion hortensis*, (b) *Arion subfuscus*, (c) *Agriolimax reticulatus*, (d) *Milax gracilis*, (e) *Milax sowerbyi*.

species, whereas the numbers active are closely associated with the weather conditions. On the other hand, the peaks in weight are dependent on both activity and physiological development.

It might be imagined that the method of collecting does not result in the young slugs being collected. But the young of all species have been collected, even tiny specimens. An explanation is that the young
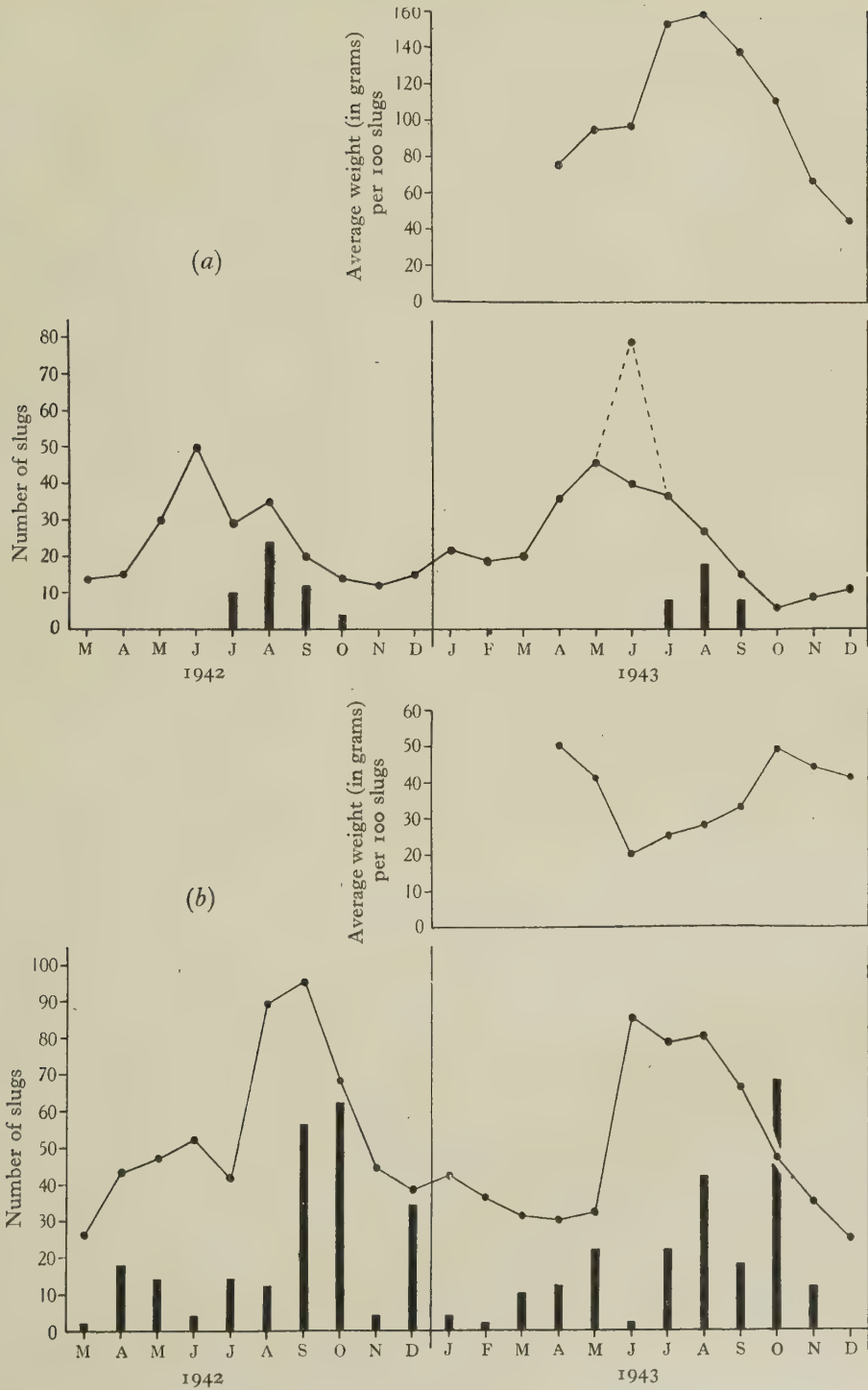
Fig. 22. Monthly activity, weight and total numbers seen mating (histograms) of (a) *Arion subfuscus* and (b) *Agriolimax reticulatus* in all gardens visited.

are not active out in the open after dark to the same extent as the older individuals at the times the collections have been made. But other workers have found that a long time may lapse between copulation and oviposition and also between oviposition and hatching.

The data for the mating of *Arion hortensis* are too sparse to allow of any deductions being made regarding this species.

(e) Weights in relation to damage

In assessing the damage liable to be done by slugs, their weights, the numbers active and the specific composition of the slug fauna should be taken into account, as well as any particular choice of food shown by any of the species and the season of the year.

From Fig. 21 (in which the monthly average weights of the five common garden species are shown in relation to the monthly average numbers found active after dark), it is obvious that with the exception of *Arion subfuscus* slugs are neither numerous nor

bad weather. But the autumn is the season of the year when certain slugs exhibit a definite food preference. In particular, *gracilis* and *hortensis* show a distinct partiality towards potato tubers and the latter species the crowns of carrots in addition. It is obvious that *gracilis* reaches its height of abundance in September and October, and it is this time of the year when the specimens are heaviest and the potato crop is available in the ground. Consequently, if *gracilis* is present to any extent in the slug fauna of a potato-growing area, great damage is liable to be incurred. Table 17 gives the percentage specific composition of collections made in the potato patches in four gardens, where serious damage to potatoes had been previously reported. In each area there was a high slug population. In the first two the present collector (H. F. B.) took the samples, whereas in the latter two the complainants collected following our instructions. It will be seen that in each area there was a high proportion of *gracilis* or *hortensis*.

Table 17. *Percentage composition of slug fauna in four garden areas in which the potato crop suffered great slug damage to the tubers*

	24 Douglas Road, Harpenden	14 The Pleasance, Harpenden	66 Norton Road, Heysham, Lancs	Marchurst, Shipbourne Tonbridge
Arion ater	1	0	0	0
A. circumscriptus	0	1	0	0
A. hortensis	61	17	29	12
A. subfuscus	1	2	0	0
Milax gracilis	31	69	66	84
M. sowerbyi	1	1	0	0
Agriolimax reticulatus	7	11	6	4

large during midsummer. Observation (§ 8) has shown that this species is prone to feed on fungi and animal faeces, although occasionally it has been seen eating lettuce, cabbage and campanula leaves. Taken as a whole, however, this species cannot be considered as a serious menace.

The other four species—*Arion hortensis, Agriolimax reticulatus, Milax gracilis* and *M. sowerbyi*— are at their heaviest in the spring and in autumn, but with the exception of *hortensis* are much more numerous in the autumn than in the spring. This means that when new growth starts to appear in the spring, gardens in which *hortensis* is a common species will probably suffer considerable damage in mild seasons (e.g. 1943), particularly to crowns of such plants as primulas and to rhizomes, for example, of Jerusalem artichokes which have been left overwinter in the ground.

On the other hand, in the autumn, when there is normally a large amount of superfluous unwanted and rotting vegetation available, a much larger slug population can usually be tolerated than in the spring when there is a comparative shortage of plant material, especially when new growth is retarded by

It is realized that *reticulatus* and *circumscriptus*, in addition to the *Milax* species and *hortensis*, have in the past frequently been associated with tuber damage. But in our experience *gracilis* is outstanding as a primary pest of potato tubers followed by *hortensis* as a fair second. *A. circumscriptus* has not been found in sufficient numbers to cause any considerable damage. *Reticulatus* in our experience is not a boring slug, and prefers to feed on green vegetable matter, e.g. potato leaves and haulms. Even when offered potato tubers, it has preferred to leave the tubers unattacked. But when once the tubers have been damaged by other agencies, e.g. cutworms, *Milax* spp., wireworms, etc., *reticulatus* will feed on them. Therefore we consider this species as liable to cause secondary damage to the potato crop.

Until further evidence is forthcoming as the result of more exact determination and abundance of the slug species involved in potato losses, we are forced to the conclusion that *Milax gracilis*, and to a much less extent *Arion hortensis*, is responsible for the major primary damage to potatoes and that *Agriolimax reticulatus* sometimes increases the losses caused by primary pests.

11. DISTRIBUTION OF SPECIES IN THE DISTRICT

One of the most interesting facts that has been brought out by this study is that the slug faunas in adjacent gardens are frequently extremely different. In other words, the fauna in one garden is no criterion of what may be expected to occur in the neighbouring gardens, either as regards total population or the relative numbers of the different species. Table 18 shows the numbers of individuals of *Arion ater*, *A. subfuscus*, *A. hortensis*, *Milax gracilis*, *M. sowerbyi* and *Agriolimax reticulatus* found in nine adjacent gardens in October 1942. The totals*

These tables show that in spite of the seasonal rise and fall in numbers which are very noticeable the distributions are maintained. Ideally in a distribution study all the localities should be sampled on the same day and at the same time, but this is impossible for one collector. Samples collected within any particular month, however, may be compared provided due precautions are taken in choosing the nights on which to collect, since the figures of seasonal activity have already shown that there is not very much change in numbers within a month. Similar tables can be drawn up for *Agriolimax reticulatus*, *Milax gracilis* and *sowerbyi*, *Arion ater* and *subfuscus* from

Table 18. *Distribution of species and total numbers in Moreton End Lane back gardens, October 1942*

Back garden No.	Arion ater	Arion hortensis	Arion subfuscus	Milax gracilis	Milax sowerbyi	Agriolimax reticulatus	Total*
5	1	185	19	93	15	63	376
7	8	56	18	73	18	95	272
9	4	60	13	36	87	75	277
11	6	11	39	17	19	94	186
13	12	9	19	5	0	56	101
15	37	4	19	6	1	50	120
17	5	35	14	9	0	59	124
19	7	30	13	33	1	49	132
21	1	123	5	38	3	92	265

Table 19. *Monthly distribution of* Arion hortensis, *1942, in Moreton End Lane back gardens*

No.	5	7	9	11	13	15
Jan.	84	57	25	—	—	3
Feb.	—	—	—	—	—	—
Mar.	66	32	25	—	9	4
Apr.	52	38	2	12	6	2
May	66	65	12	6	3	2
June	18	13	—	—	2	1
July	24	11	0	1	0	0
Aug.	81	10	7	0	0	0
Sept.	150	50	20	8	0	1
Oct.	185	56	60	11	9	4
Nov.	162	105	89	48	19	18
Dec.	187	164	109	37	22	22

Table 20. *Monthly distribution of* Arion hortensis, *1943, in Moreton End Lane back gardens*

No.	5	7	9	11	13	15
Jan.	143	69	56	23	—	20
Feb.	113	72	18	10	—	4
Mar.	101	82	16	7	—	3
Apr.	81	54	60	4	—	16
May	59	34	22	2	3	9
June	18	5	5	0	—	3
July	8	3	0	1	—	0
Aug.	34	6	3	2	—	0
Sept.	88	38	2	(5)	—	1
Oct.	160	65	82	21	17	13
Nov.	125	44	81	15	—	23
Dec.	86	—	47	—	—	27

include all the species found. It will be seen that most individuals of *A. ater* were found in No. 15 and there are indications that the numbers increase from No. 5 to garden No. 15 and then drop again. In the cases of *A. hortensis* and *M. gracilis* there is a decrease in numbers as one goes from No. 5 to No. 15, but then the numbers increase again. The distribution of *M. sowerbyi* is different. This species is most abundant in No. 9 and only just present in Nos. 13–21. Lastly, *A. subfuscus* and *A. reticulatus* appear to be randomly distributed throughout these gardens.

Tables 19 and 20 give the figures month by month in Nos. 5, 7, 9, 11, 13 and 15 for *A. hortensis* throughout 1942 and 1943. The peculiar distribution appears to be constant for the two years.

Appendix 1 and these confirm the distributions shown in Table 18.

This series of observations spread over two years shows that the numbers of certain species have remained different from garden to garden, certain gardens having more individuals active than others throughout the year at any point on the seasonal activity curve of the particular species. In addition, the relative proportions of one species to another have remained different. For example, the relative proportions of *Arion hortensis* to *A. subfuscus* are consistently higher in No. 5 back garden than in No. 15 throughout the seasons, notwithstanding the very different numerical abundance from month to month (Fig. 23). In addition, these curves are further evidence of the adequacy of the sampling technique.

They indicate that the fluctuations in numbers from collection to collection (see Part 1, Figs. 3, 6) are due more to weather changes than to sampling, in that the fluctuations in the ratios are much less pronounced. The latter fluctuations are probably chiefly made up of the sampling error and any differential effect of weather changes on the two species.

The marked distributions shown to exist must be due to some definite cause. The most obvious controlling agencies of animal populations include food supply, natural enemies and the physical conditions obtaining in the habitat.

In the first place owing to the varied tastes of slugs it is not easy to believe that food is the limiting factor. In this connexion it should be mentioned that, although the numbers of *A. hortensis* in No. 15 Moreton End Lane are the lowest, the average weights of this species during the four months (October–January) were distinctly bigger in this garden than in No. 5

There remains the probability that some soil condition is responsible for these remarkable distributions. It seems probable also that these conditions are deep rooted rather than superficial.

The pH of the soil was tested, but there was no clear-cut gradation in the acidity or alkalinity of the surface soil. Thanks to the kindness of Mr R. G. Warren of the Chemistry Department at Rothamsted Experimental Station figures were obtained for the organic carbon in the soil as shown below (Table 21). It will be seen that this cannot account for the slug distribution.

Neither can the amount of cultivation and care a garden receives be held wholly responsible, although this does affect the total numbers from sample to sample at certain times of the year but not the relative abundance of the species.

Mechanical analysis of the soils, which was done for us in the Physics Department at Rothamsted
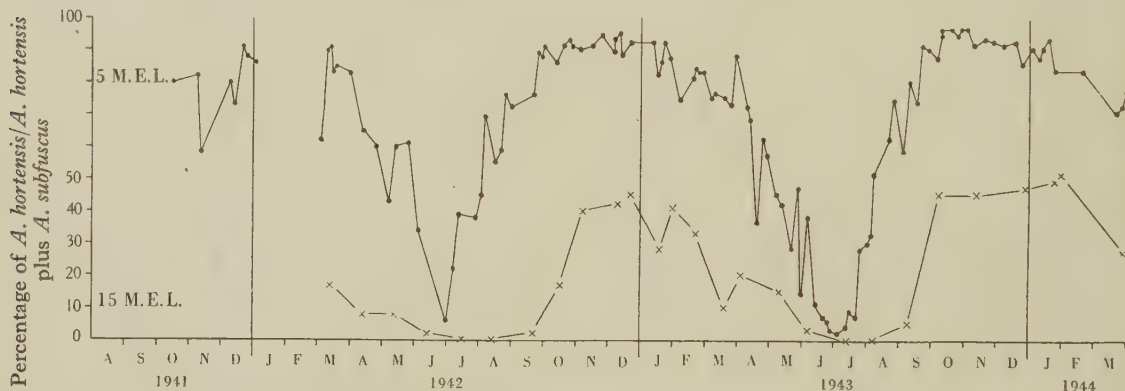
Fig. 23. Ratio of *Arion hortensis* to *A. subfuscus* (expressed as a percentage) in the back gardens of Nos. 5 and 15 Moreton End Lane.

Moreton End Lane where this species was so much more abundant. In fact, the weight data indicate that the fewer the slugs collected the bigger and heavier the specimens. But the relative numbers have remained constant.

No evidence has pointed to the possibility that natural enemies control the slugs differentially with such regularity in the various gardens. Again, our experience indicates that weather, even in the severe winter of 1941–2, has no lethal effect on slugs.

The back gardens in Moreton End Lane vary in the numbers of trees, for example Nos. 5 and 15 have a considerable number, especially No. 5, while in Nos. 9, 11 and 13 the largest trees are a few young fruit trees. Thus there is no gradient of shade from garden to garden. Each garden has completely mixed flora of ornamental and the usual culinary plants. Thus there is no reason to connect the observed distribution of slugs with the flora. As regards lay-out the gardens are roughly the same—each having a rockery, rubbish heap, rose beds, perennial borders, vegetable patches, lawn, paths and so on.

Table 21. *Organic carbon in Moreton End Lane back gardens*

Back garden No.	% organic carbon
5	3·13
7	2·62
9	2·78
11	2·67
13	2·56
15	3·02

Experimental Station, thanks to the courtesy of Dr R. K. Schofield, revealed no appreciable differences. Table 22 gives these figures on the oven-dry basis.

The same types of distribution are similarly apparent in the front gardens of the same properties. The front and back gardens are usually separated by gravel or concrete narrow paths between the wooden fences demarking the property and the houses. Table 23 gives the numbers of the same six species in six of the nine front gardens.

Harpenden is situated in the part of Hertfordshire that is made up of chalk overlaid by clay with flints.

River valleys are cut through the clay with flints, exposing the chalk on the flanks of the valleys. Luton Road lies on the course of an old stream bed which is here represented by a valley. flat made up of river gravel and alluvium. Moreton End Lane, a turning off Luton Road, goes up the side of this valley and, higher up, the lane passes on to the clay with flints. It is not yet known how much cover there is over the chalk along the flank of the valley between the river gravel at the bottom and the clay with flints at the top.

In order to test whether the underlying geological formation was connected with the species distribution, samples were taken during 1943 in the gardens

Table 22. *Mechanical analysis of the soil in six Moreton End Lane back gardens*

No.	5	7	9	11	13	15
Coarse sand	15·9	17·5	18·3	18·1	21·2	14·2
Fine sand	38·1	37·1	35·8	34·6	33·7	39·5
Silt	22·7	20·5	19·3	18·7	16·3	20·5
Clay	18·3	17·3	18·5	21·7	21·0	19·5
Carbonates:						
Air-dry soil	2·3	2·4	2·6	2·8	2·6	2·4
Loss by solution	1·2	1·4	1·4	1·1	1·1	1·2
Difference	+1·5	+3·8	+4·1	+3·0	+4·1	+2·7
Total	100	100	100	100	100	100

Table 23. *Distribution of six species of slugs in six front gardens in Moreton End Lane, October 1942*

No. of front garden	Arion ater	Arion hor-tensis	Arion sub-fuscus	Milax gracilis	Milax sower-byi	Agrio-limax reticu-latus
5	0	114	16	97	2	60
7	6	43	13	24	7	60
9	0	6	6	5	10	90
11	3	23	13	7	7	109
13	8	4	12	10	2	80
15	12	6	10	13	1	62

in the neighbouring roads, which go over the same formations. Figs. 24–29 show the numbers of *Arion ater, A. hortensis, A. subfuscus, Milax gracilis, M. sowerbyi* and *Agriolimax reticulatus* which were obtained in May and June 1943.

Arion ater (Fig. 24) was found in greater numbers in Moreton Place gardens, which back on to the wooded railway embankment, but was practically absent from those in Douglas Road and on the east side of Luton Road. The distribution of this species may be associated with the amount of coarse grass both in and near the particular garden. Thus there is an uncultivated patch of grass just west of the top of Moreton Place and the largest numbers of *ater* are to be found in near-by gardens. But this may not be the whole explanation, since the gardens on the south side of Douglas Road adjoin a meadow. The age of

the garden may also be a factor. Thus the gardens of Moreton End Lane and Moreton Place are of more recent origin than those on the east side of Luton Road and those in Douglas Road.

The distributions of *Arion hortensis* (Fig. 25) and *Milax gracilis* (Fig. 26) are most interesting. At the lower or east end of Douglas Road, Moreton End Lane and Moreton Place the numbers are high, decreasing as one proceeds up the slope until (at No. 20 Douglas Road and No. 17 Moreton End Lane) the numbers become large again. There is a distinct band across the roads where the numbers are low. The similarity in distribution of these two species again suggests some connexion between their ecology.

As a contrast there seems to be a belt of high numbers of *Milax sowerbyi* (Fig. 27) running from No. 9 Douglas Road across to No. 16 Douglas Road across to No. 9 Moreton End Lane and No. 5 Moreton Place. In addition high numbers of this species occur in certain Luton Road gardens.

The distribution of *Arion subfuscus* (Fig. 28) reveals no such bands of abundance, but it is much commoner in the Moreton End Lane and Moreton Place gardens than are found in the Douglas Road gardens and still less are found in the Luton Road gardens. This grouping follows the age of the gardens, the Luton Road ones being the oldest, followed by those in Douglas Road, while those in Moreton End Lane and Moreton Place are the most recent. As regards its almost complete absence in the gardens on the east side of Luton Road, one is tempted to recall the map (Pl. 20) showing the distribution of this species in Taylor's volume of slugs (1907, p. 208). In this *subfuscus* is shown as being absent from the following counties: Buckinghamshire, Bedfordshire, Hertfordshire, Huntingdonshire, Cambridgeshire, Norfolk and Essex. (It is as well to recall that this 'absence' is based on collectors' records. It is quite possible that more extensive sampling at the most favourable season of the year would reveal this species' presence, though not abundance, throughout these eastern counties.)

It can be suggested that since the year of publication of this map, the distribution of *subfuscus* has advanced eastwards and that this species is now well established on the west side of the Luton Road which runs roughly north and south through Harpenden. *A. subfuscus* occurred in 165 out of the 167 samples taken throughout 1942 in gardens on the west side of this road, but not once in the three samples taken in gardens on the east side of the road. In 1943 the comparative figures are *subfuscus* present in 162 out of 164 samples taken on the west side, but only in two out of 17 samples taken on the east side. Emphasis is laid on 15 of these 17 samples having been taken in May and June when *subfuscus* was at its peak of numbers in the gardens on the west side. Another perhaps more reasonable suggestion to account for its absence from the eastern counties

Fig. 24. Numbers of *Arion ater* per sample in the Moreton End district of Harpenden during April (figures asterisked), May, and June (figures in italics), 1943.

N

6

2

75

9
3
2
22.
34
59

21

Douglas Road

Moreton End Lane

35
34
134
157
116
193*
171

5

6
4

6

28

6

32

113

Moreton Place

51

28

Luton Road

Clarence Road

5

30*

4 3 7 15 3 23 1 16

3

0   100   200   300 feet

Fig. 25. Numbers of *Arion hortensis* per sample in the Moreton End district of Harpenden during April (figures asterisked), May, and June (figures in italics), 1943.

Fig. 26. Numbers of *Milax gracilis* per sample in the Moreton End district of Harpenden during April (figures asterisked), May, and June (figures in italics), 1943.

N

6

6

1

6

6

1
2
4
25
15

8

42

71
24
7
16
2
1*
6

Douglas Road

Moreton End Lane

11

4

21

17

63

28

Moreton Place

12

4

17
15

Luton Road

Clarence Road

60

22*
16 13 32 59 58 36 27 26

8

0   100   200   300 feet

Fig. 27. Numbers of *Milax sowerbyi* per sample in the Moreton End district of Harpenden during April (figures asterisked), May, and June (figures in italics), 1943.

N

Fig. 28. Numbers of *Arion subfuscus* per sample in the Moreton End district of Harpenden during April (figures asterisked), May, and June (figures in italics), 1943.
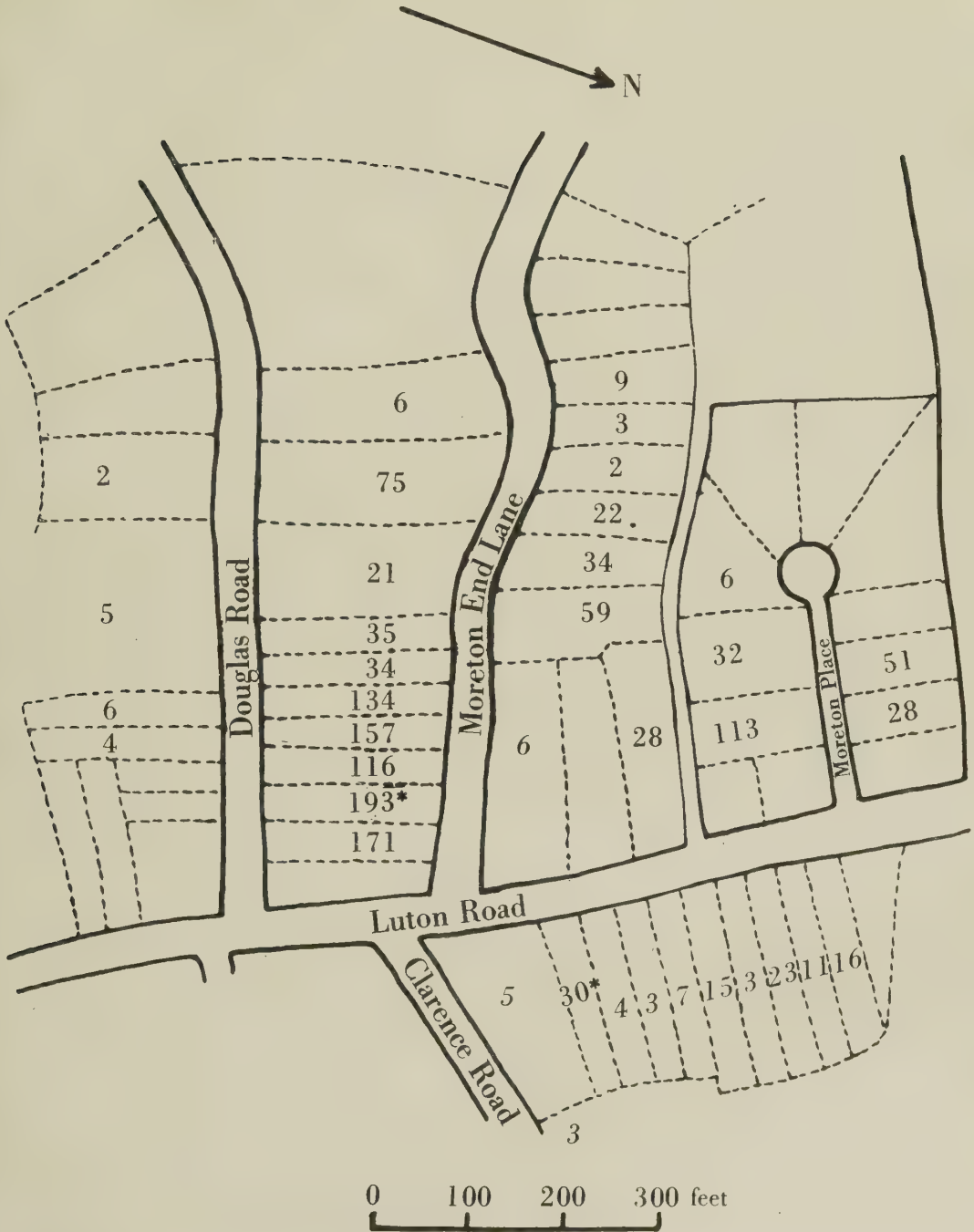
Fig. 29. Numbers of *Agriolimax reticulatus* per sample in the Moreton End district of Harpenden during April (figures asterisked), May, and June (figures in italics), 1943.

may be found in the fact that this species reaches its peak of activity and mating in the summer. It has already been stated that it is surprising to find the peak of any slug during what is normally warm dry weather. It may be that the summer in the eastern counties is too dry for successful annual replenishment of the species, i.e. by mating, oviposition and hatching, whereas in the rest of the country there is usually enough moisture in spite of the temperature being at its highest. There is evidence (Part 1, Fig. 6) that a real drought in the height of summer does reduce activity in this species.

The distribution of *Agriolimax reticulatus* (Fig. 29) was found to be as expected, i.e. it occurred everywhere and there were no obvious differences in any garden or sets of gardens.

Limax maximus seems to occur in small numbers in many gardens, but in two gardens (Nos. 74 and 76 Luton Road) exceptionally high numbers for this species were found.

The gradients shown in the numbers of *Arion hortensis* and *Milax gracilis*, as well as the ridge in abundance of *M. sowerbyi*, may indicate that the soil and underlying formation is a factor influencing the abundance of these species.

Another possible explanation of the distributions of the slug species may be revealed when the moisture retention properties of the soil in the various gardens have been examined. Also spectroscopic examination of the soils may reveal some striking differences, for example in the presence or quantities of some of the rarer elements, sufficiently clear cut to be associated with these observed distributions of the slug species.

The importance of discovering the explanation becomes apparent as soon as control measures are envisaged.

12. TIME OF NOCTURNAL ACTIVITY

It is well known that slugs are largely nocturnal in their habits, but that under special circumstances they do become active to some extent during the daytime. It is obvious that, for such a study as this, involving the observation and collection of active slugs, as well as for the interpretation of baiting and trapping experiments, it is essential to have more exact information regarding their periods of activity. It has, for example, already been pointed out (Part 1, § 4) that collecting should be done at an hour when all the species are fully active. In order to do this it is necessary to have partial answers at least to such questions as the following: does each species become active at the same time and is the duration of its activity period the same, do the young and old of a species behave in the same manner, is the period of activity dependent chiefly on the duration of the night, i.e. longer on the long winter nights than on the short summer ones, and controlled by the times of sunrise and sunset, and does the whole slug

population automatically become active (atmospheric and soil conditions permitting) each day as the light fails or are the slugs active only when in need of food, etc.? If the latter were true, it would indicate that a much greater proportion of the population could be expected to be active on any suitable night during the winter and summer months when favourable nights are relatively more infrequent than on similar nights during the spring and autumn when the chances of a sequence of nights favourable to slug activity are correspondingly much greater. This implication, if proven, would be of the utmost importance in any attempt to estimate population figures from activity numbers.

The first definite indication that species of slugs might have different times of nocturnal activity in relation to the season of the year was obtained in the early baiting experiments (Barnes & Weil, 1942). The proportion caught on the baits before and after midnight varied, fewer before midnight in the spring than in the early autumn. This gave rise to the suggestion that different species of slugs had different times of nocturnal activity and that different species predominated in the garden at different seasons of the year. This latter has subsequently been proved. The slugs attracted per hour throughout one night (30–31 August 1941) to heaps of three baits (bran only, bran mixed with powdered metaldehyde and powdered metaldehyde alone) were counted after removal. Fig. 2 (loc. cit.), in which these numbers are shown, clearly indicates that on this particular August night (sunset 18.58 hr. G.M.T.) slugs began to be active between 18.30 and 19.30 hr., that the greatest numbers were active (i.e. attracted to the baits) between 19.30 and 20.30 and that after this the numbers fell off rapidly until 5.30 hr. the next morning. Unfortunately the slugs were not identified specifically until September 1941, so these facts can only be taken to refer to slugs as a group. But from our more recent work on seasonal activity it can be safely judged that large numbers of *Agriolimax reticulatus* would have been active that night.

In 1942 an attempt was made to get exact data on the numbers of the different slugs species active throughout the night during June. Accordingly ten replicated heaps of bran only were placed at different points in the back garden of No. 5 Moreton End Lane at 12.00 hr. on 13 June. The numbers of slugs seen at these heaps at various times throughout the next 48 hr. were recorded. The slugs were allowed to remain on the heaps and were not removed. The figures are given in Table 24.

It will be seen that the duration of the activity periods of the various species is not the same, different species being active for longer or shorter periods and some starting earlier, others later. Their times of activity on these two successive nights were surprisingly similar, although there were more of each species, except *Arion hortensis* and *Milax*

sowerbyi, active on the second night. Thus, for example, appreciable numbers of *hortensis* were active each day both before sunset and after sunrise as well as throughout each night, whereas the other species had shorter periods of activity. In fact, the bulk of the slug fauna active up to sunset and from dawn onwards consisted of this species. Likewise, there is evidence that *Agriolimax reticulatus* reaches its peak of activity before midnight, *Arion subfuscus* at about midnight and *Milax gracilis* after midnight. Taken as a group it would appear that the majority of the slugs were active by 2 hr. after sunset and remained so until 2 hr. before sunrise.

It remains to be proved whether these times of activity of the different species remain relatively constant throughout the seasons of the year and also whether or not these actual times, in relation to sunrise and sunset, are the same during the long winter nights.

By observation the impression had been gained that slugs do not come out so soon after sunset in the middle of winter as they do in the height of summer. But the only numerical evidence that it has been possible to obtain is given in Table 25.

When the bran baits were put in position on 27 December the weather was mild and the sky overcast, but very soon after the sky cleared and the temperature fell from about 41° F. at 15·15 hr. to about 37° F. at 19·15 and about 32° F. in patches at 21.15 hr. The night of 2–3 January was favourable for slug activity, but it was not found possible to continue the observations throughout the night. So that, although there was no appreciable slug activity on these two occasions until the third hourly count after sunset (compared with the one at sunset or the first one after during June, see Table 24), it would not be wise to conclude that this was proof that slugs become active later in relation to sunset in the winter than in the summer. Further evidence must be obtained.

But it seems clear that for the present, if the method of collecting after dark all visibly active slugs is adopted as a sampling method, such collections should be made not earlier than 2 hr. after sunset nor later than 2 hr. before dawn at least during June, nor earlier than 3 hr. after sunset in December. Otherwise the relative numbers of *Arion hortensis* would be too high in proportion to the other species and also the numbers of all species at such an early or late hour would give an unnecessarily inaccurate idea of the total numbers active on that particular night.

These times of activity are also most important when a comparison is made of different sampling methods. For example, the times of activity must influence the proportion of the various species found on any baits or traps that are examined the next morning, since there is a much longer period each night (at least in June) during which *Arion hortensis*

can be attracted to, or by chance come within the range of attraction of, the bait than, for example, *A. subfuscus*. Consequently, results might tend to show that *hortensis* was more attracted to the bait or caught by the traps than *subfuscus*, although in reality a higher percentage of the available *subfuscus* might have been attracted or caught.

On six occasions during 1942 half-hour collections were made around sunset in the back garden of No. 5 Moreton End Lane and once at dawn. No electric torch was used in these collections, otherwise they were carried out in the same manner as the after-dark collections. Full details are given in Table 26. In the evening collections the bulk of the slugs of all species were quite small and this was in great contrast to the normal nightly collections, although small slugs were collected after dark but not in such overwhelming proportions. The second outstanding feature is the steady decrease from May to December in the total number as well as those of the individual species. It seems unlikely that this decrease is purely fortuitous. The diminution of *hortensis* (virtually all immature or 'babies') is most striking, especially when considered in relation to the seasonal activity curves of this species obtained by collecting after dark. The decrease may be linked up with the rate of breeding.

13. RESTRICTION OF ACTIVITY BY VARIOUS WEATHER CONDITIONS

In such an observational and essentially field study as this, there have been many opportunities of seeing how slugs behave under various weather conditions. The more one sees, the more obvious it becomes that no single factor or even simple combination of factors is ever at work. It is the result of these complex combinations, or the weather conditions changing, that the numbers of active slugs vary from time to time.

In this section examples will be given of the numbers of slugs found active under various conditions. These examples are for convenience grouped under the most obvious prevailing factor, such as cold, drought, falling rain, warmth and wind. But it must be appreciated that in each case a host of other physical factors is at work, sometimes dependent on the prime factor involved, at others quite independent. For this reason it is impossible to state specifically the exact cause of every sudden increase or decrease in the numbers of slugs active in the field.

Under laboratory conditions the effect of particular and simple combinations of factors can be disentangled. But it seems that it would be usually well-nigh impossible to apply these results out in the garden, because in the first place the various combinations in the field are so very complex and there is no instrument available by which the weather as such can be measured. Secondly, there is little uniformity

Table 24. *Number of slugs seen at, but not removed from, baits of bran only on* (a) 13–14 June *and* (b) 14–15 June 1942 *(sunset 20.15 hr.: sunrise 3.45 hr.). The baits were placed in position in the back garden of No. 5 Moreton End Lane at 12.00 hr. on 13 June*

Species		13.15	16.15	19.15	20.15	21.15	22.15	23.10	00.50	1.45	2.45	3.45	4.45	5.45	7.45	10.45	Total seen
								Hour (G.M.T.)									
Arion ater	(a)	0	0	1	1	5	8	—	—	4	5	2	0	0	0	0	26
	(b)	—	0	0	0	1	5	8	4	4	2	2	2	2	0	—	30
A. circumscriptus	(a)	0	0	0	0	0	3	—	—	1	1	1	1	0	0	0	7
	(b)	—	0	0	0	1	4	5	3	2	1	0	0	0	0	—	16
A. hortensis	(a)	8	7	13	28	36	43	—	—	44	51	43	52	20	5	2	352
	(b)	—	3	13	23	30	34	41	38	37	29	23	37	22	13	—	343
A. subfuscus	(a)	1	0	0	1	16	37	—	—	59	38	15	8	4	2	0	181
	(b)	—	0	0	2	24	31	40	43	33	25	5	3	3	0	—	209
Milax gracilis	(a)	0	0	0	1	12	19	—	—	22	19	2	1	0	0	1	77
	(b)	—	0	0	4	8	11	14	17	17	8	4	1	1	0	—	85
M. sowerbyi	(a)	0	0	0	0	0	3	—	—	9	3	0	0	0	0	0	15
	(b)	—	0	0	0	2	1	3	4	3	2	0	0	0	0	—	15
Agriolimax reticulatus	(a)	1	1	0	2	5	10	—	—	13	7	5	3	1	0	0	48
	(b)	—	0	0	0	8	20	21	16	13	6	4	4	2	0	—	94
Total	(a)	10	8	14	33	74	123	—	—	152	124	68	65	25	7	3	706
	(b)	—	3	13	29	74	106	132	125	109	73	38	47	30	13	—	792

Table 25. *Number of slugs seen at, but not removed from, baits of bran only on* (a) 27 December 1943 *(sunset 15.57 hr.) and* (b) 2–3 January 1944 *(sunset 16.03 hr.). The baits were placed in position in the front garden of No. 5 Moreton End Lane at 12.00 hr. on 27 December and the same baits were used on 2–3 January*

Species		13.15	14.15	15.15	16.15	17.15	18.15	19.15	20.15	21.15	22.15	23.15	00.15	1.15	8.15	Total seen
								Hour (G.M.T.)									
Arion ater	(a)	0	0	0	0	0	0	0	1	1	1	—	—	—	—	3
	(b)	—	—	0	0	0	0	0	0	0	0	1	2	1	0	4
A. circumscriptus	(a)	0	0	0	0	0	0	0	0	0	0	—	—	—	—	0
	(b)	—	—	0	0	0	0	0	0	1	2	1	0	0	0	4
A. hortensis	(a)	1	1	1	1	0	10	10	7	12	10	—	—	—	—	53
	(b)	—	—	0	0	2	12	23	26	30	24	18	21	21	5	182
A. subfuscus	(a)	0	0	0	0	1	7	12	10	7	5	—	—	—	—	42
	(b)	—	—	0	0	2	15	18	26	30	21	18	17	14	0	161
Milax gracilis	(a)	1	—	0	2	4	9	11	6	9	9	—	—	—	—	51
	(b)	—	—	0	0	3	9	7	8	9	12	16	16	19	3	103
M. sowerbyi	(a)	0	—	0	0	0	0	0	0	0	0	—	—	—	—	0
	(b)	—	—	0	0	0	0	0	0	0	0	0	0	1	0	1
Agriolimax reticulatus	(a)	0	0	0	0	2	9	11	10	5	4	—	—	—	—	41
	(b)	—	—	0	0	1	11	17	20	21	17	12	14	15	0	128
Total	(a)	2	1	1	3	7	35	44	34	34	29	—	—	—	—	190
	(b)	—	—	0	0	8	47	65	80	91	76	66	70	71	8	583

Table 26. *Numbers of slugs collected during twilight at sunset and at dawn, No. 5 Moreton End Lane, 1942*

Date	Time of collection (30 min.)	Arion ater	Arion circum-scriptus	Arion hortensis	Arion subfuscus	Milax gracilis	Milax sowerbyi	Agrio-limax reticu-latus	Limax maximus	Total
				At sunset						
22 May	19.30–20.00	5	1	249	6	58	0	7	0	326
25 May	19.25–19.55	1	1	208	7	14	0	6	0	237
5 June	20.00–20.30	1	0	74	11	19	1	16	1	123
23 Aug.	18.45–19.15	0	0	49	0	10	0	1	0	60
29 Sept.	17.30–18.00	0	0	18	0	7	0	3	0	28
22 Dec.	15.45–16.15	0	0	0	0	0	0	1	0	1
				At sunrise						
7 June	4.15–4.45	1	3	81	6	5	0	11	0	107

Note. Sunset: 22 May, 19.54 hr.; 25 May, 19.58 hr.; 5 June, 20.11 hr.; 23 Aug., 19·08 hr.; 29 Sept., 17.44 hr.; 22 Dec., 15.54 hr. Sunrise: 7 June, 3.45 hr.

of conditions outside, particularly in gardens and on allotments. Even in fields the lack of uniformity of such conditions is obvious if one considers micro-climates and, after all, it is probably these that account for slugs being active or not.

(a) *Activity during cold spells and immediately afterwards*

There is no slug activity when it is actually freezing. During periods when the day and evening temperatures are moderate and there are frosts each early morning, full activity goes on during roughly the first half of the night but ceases during the latter half. Thus, 289 slugs (comprising the normal number of each species of this season of the year) were collected between 21.00–21.30 hr. of 20 February 1943, although the minimum grass temperature early that day had been 26·6°F. and early on the next morning it was 25·6°F. These tempera-

parts of a garden even when a frost is already settling in the more exposed parts of the same garden. But all activity ceases as soon as the frost becomes general.

After short periods of cold weather, the slugs quickly resume full activity. Thus, after the cold spell, 26–31 December inclusive at the end of 1941, there was full activity on the evening of 2 January 1942. After prolonged periods of cold, the speed of resumption of full activity is equally striking. In 1942 there was an unusually severe and prolonged cold period from 6 January until 14 March inclusive during which the minimum grass temperature was above 32°F. on only four nights (25 and 26 January, 4 and 12 March). On 2 January, just before this cold spell started, 181 slugs were collected in half an hour. On 14 and 15 March, immediately after it had ended, 182 and 187 slugs respectively were collected per half hour. The numbers of the various species comprising these samples were:

Date	Arion ater	Arion circum-scriptus	Arion hortensis	Arion subfuscus	Milax gracilis	Milax sowerbyi	Agriolimax reticulatus	Limax maximus	Total
2 Jan.	5	4	84	14	37	4	32	1	181
14 Mar.	3	0	99	20	35	4	20	1	182
15 Mar.	2	2	106	19	28	6	24	0	187

tures were not recorded actually in the garden involved, but there were certainly appreciable frosts.* The evening of 6 March 1943 was quite similar. In the early morning the temperature had fallen to 29·3°F. and the following morning 20·4°F. was recorded, but slugs of all species were fully active on the evening of the 6th, 288 slugs being collected between 20.35–21.05 hr.

It has also been observed frequently that some slugs may still be found active in the more sheltered

* All the collections of slugs referred to in this section were done in the back garden of No. 5 Moreton End Lane and all the temperatures are those recorded at Rothamsted Experimental Station. Specific analyses of the slug captures are given in Appendix 1.

Similar results were obtained in other gardens (see Appendix 2). It is thus obvious that after even such a prolonged period of unusual cold the same numbers of slugs are active as before. This proves conclusively that one cannot depend on cold winters in England destroying slugs. It also indicates that slugs can take up positions where fairly intense and certainly prolonged cold does not reach them sufficiently to decimate their numbers.

During this cold spell a few observations were made to see what effect a slight thaw had on slug activity. Thus, on 24 January, when the minimum night temperature was a fraction of a degree above freezing, a half-hour collection was made between 20.20 and 20.50 hr. It was not freezing at this time

but snow was covering all the ground except for small patches round plants and there was none on the rubbish heap. 31 slugs (3 baby *Arion ater*, 9 *A. subfuscus* and 19 *Agriolimax reticulatus*) were found, of these all except two or three (*reticulatus*) were found on the rubbish heap, which was largely composed of the autumnal leaves. Again, the following night when it was freezing (21.20–21.50 hr.) except on the rubbish heap, no slugs could be found except one *Arion hortensis* and two *Agriolimax reticulatus* which were on the rubbish heap. On 4 March, with the minimum temperature again a fraction of a degree above freezing, 32 slugs (10 *Arion hortensis*, 6 *A. subfuscus*, 1 *Milax gracilis* and 15 *Agriolimax reticulatus*) were collected. Similarly, on 11 and 13 March, 60 and 56 slugs respectively were collected in half-hour periods. This was followed by the full numbers being active again on 14 March as already stated.

More information on the activity of the various species during cold spells has already been given in the sections dealing with the abundance and seasonal activity. One cannot help gaining the impression that the species may be arranged roughly in the order of their apparent resistance to cold. The most resistant, to all weather changes considered together, appears to be *Agriolimax reticulatus* followed by *Arion subfuscus*, *A. ater* and *Milax sowerbyi* come next, while *M. gracilis* and *Arion hortensis* appear to be most susceptible.

The return of the species to activity after severe cold probably depends to some extent on the depth under leaves and in the soil at which the different species take cover. Thus *reticulatus* seems to take up comparatively superficial positions and so would be able to resume activity almost immediately a thaw set in. On the other hand, *gracilis* goes definitely into the underlying soil, so temporary thaws at the surface of the ground would not necessarily penetrate the soil down to where *gracilis* was taking cover and the thaw would have to be more prolonged to enable full activity of this species to be resumed.

For this reason it is not wise to be too dogmatic in stating that the different species have different susceptibilities to cold. Only laboratory experiments could decide this. Carrick (1942), after experimenting with *reticulatus*, comes to the conclusion that 'normal extremes of weather in Britain are not usually lethal to *A. agrestis* [*A. reticulatus*], but they do serve to inhibit adult activity and reproduction'.

(b) *Activity in periods without rain and soon after*

The activity of slugs has been reduced during rainless periods at certain periods of the year, but at others it seems to have been almost unaffected. The recovery rate after such periods also seems to have changed with the season of the year.

The following examples taken from after-dark sampling in the back garden of No. 5 Moreton End Lane illustrate this. The full analyses of the numbers of the individual species are to be found in Appendix 1.

1. On 21 and 23 February 1943, 6 and 8 days after 0·014 in. of rain on 15 February, 210 and 127 slugs were collected in 30 min. compared with 289 on 20 February, which was 5 days after any rain. There was 0·018 in. of rain at about 16.00 hr. on 25 February and the same evening between 21.20 and 21.50 hr. 261 slugs were collected. This small amount of rain apparently was sufficient to enable full activity to be resumed on this night.

2. On 6 March 1943 288 slugs were collected although it was 9 days since any rain had fallen, but on 8 March (11 days since any rain) only 133 were collected. However, on 6 March dew had fallen by the time the collection was started at 20.35 hr. and the surface was quite moist, whereas on 8 March no dew had fallen by the time of collecting (20.20 hr.) and the surface was dry. On both occasions the water content of the soil was high.

3. On 24 April 1942, the fifteenth day since any rain (0·214 in., 9 April), only 56 slugs were collected and on 7 May, the twenty-eighth day since rain, only 83 slugs were collected. Previous to this drought period 230 slugs were collected in a sample on 12 April. One day after the drought was broken, by 0·548 in. rain on 10 May, 258 slugs were collected. In this case apparently full activity was resumed the night after the drought was broken.

4. On 4 June 1942 (5 days after 0·135 in. rain on 29 May) 243 slugs were collected. On 30 June (18 days since 0·175 in. rain on 12 June) only 103 slugs were found. In this case the recovery to normal numbers being active was not immediate as in the two previous cases (in February and April). Rain fell on 3 days (0·012 in. on 3 July; 0·029 in. on 4 July and 0·019 in. on 6 July), but only 140 slugs were collected on the evening of 6 July. Again, after further rain (0·148 in. on 7 July; 0·160 in. on 9 July; and 0·270 in. on 10 July), 193 slugs were collected on the evening of 10 July. By 27 July nearly 1·5 in. rain had fallen (on 8 days) and the numbers of slugs collected on 27 July was 212, thus practically reaching the number (243) collected before the rainless period in June.

The following deductions seem justifiable from these data. During the earlier part of the year when there is plenty of moisture in the soil, following the winter rains and snow, a very slight amount of rain (e.g. Example 1) is sufficient to cause full activity to be resumed after a rainless period. In addition, at this season of the year, the breaking of a drought is followed by an immediate resumption of full activity (e.g. Examples 1 and 3). Even heavy dew during a rainless period early in the year enables full activity

to be resumed (e.g. Example 2). Later, in the summer when the water content of the soil is lower, full slug activity is not resumed immediately rain has fallen (e.g. Example 4).

It would appear that slug activity depends ultimately on there being a film of moisture over the places where they are going to be active. If this is absent, activity is curtailed, even although there may be plenty of moisture in the soil. This has been frequently demonstrated by the fact that on nights when concrete paths are dry but the soil on either side is moist, the slugs are active on the soil but not on the path. But immediately the surface of the path becomes moist by slight rain many slugs can be seen moving across it and feeding on anything, such as dead leaves, which they can find upon it. Again, even when there is plenty of surface moisture, the slugs cannot be active unless the moisture reaches them wherever they happen to be.

(c) Activity while rain is falling

When heavy rain is actually falling the number of slugs found active has been reduced. The following example is given of half-hour collections made in the same garden on successive nights when apparently the only difference in conditions was that on one night rain was actually falling heavily all the time the collection was being made and on the next there was no rain.

Table 27. *Comparison of the numbers of slugs active (A) during heavy rain, (B) no rain falling (No. 10 Douglas Road)*

	A 5 Oct. 42	B 6 Oct. 42
Arion hortensis	45	268
A. subfuscus	7	5
Milax gracilis	23	73
M. sowerbyi	1	12
Agriolimax reticulatus	24	79
Total	100	437

On the other hand, when slight gentle rain is falling there seems to be no appreciable reduction in the numbers of active slugs. And usually immediately after rain has ceased falling an increase in numbers is obvious.

(d) Activity during hot spells

Carrick (1942) found that *Agriolimax reticulatus* was only slightly active under laboratory conditions at 77° F., although it could exist at 86° F.

In the present study no temperatures approaching these were encountered, as the night temperatures have always been lower. But during the summer of 1942 reduced activity of the slugs occurred during June and July. In addition to the normal decrease in the numbers of certain species which are active at

this time of the year, it is considered that this lack of activity was partly due to unfavourable conditions concerning moisture rather than to the summer temperatures prevailing at that time. No evidence has been obtained that heat, as such, is responsible for immobilizing slugs in the field and in fact conditions for such a possibility to occur must be extremely unlikely to obtain in this country.

It is concluded that any diminution of slug activity in this country during hot weather is not due to the actual temperature, but to increased evaporation causing drought conditions to obtain on the surface and in the surface layers of the soil.

(e) Activity in heavy wind

It has been observed that on windy nights fewer slugs are active than usual. Often wind results in a reduction in temperature and what is more important a drying out of the surface layers of the soil. On the other hand, the wind may be definitely moisture-

Table 28. *Comparison of the numbers of slugs active (A) on a damp windy night, (B) on a damp still night*

	A 5 Dec. 42	B 6 Dec. 42
Arion ater	2	2
A. circumscriptus	0	1
A. hortensis	102	183
A. subfuscus	13	13
Milax gracilis	32	95
M. sowerbyi	5	7
Agriolimax reticulatus	22	28
Total	176	329

bearing and it is then that the true effect of wind on the activity of slugs is observable. Table 28 gives the results of sampling on a damp windy night and on a still night in December. The wind was very strong, but of course there were plenty of places, e.g. behind bricks, perennial plants, etc. where its full force could not have been felt. Observation showed that few slugs were active in exposed places and most of the slugs collected were found in sheltered sites. This would account for the comparatively large numbers of slugs to be found in gardens during heavy damp winds. On the other hand, the full effect of wind would be seen in exposed fields.

14. SUMMARY

Section 8. Observations of slugs feeding in gardens indicate that very little of their food consists of plant material grown for human consumption or pleasure. In places where one crop only is grown, e.g. potato patches in the autumn, the damage would be higher owing to the absence of alternative food.

Section 9. Mating of *Agriolimax reticulatus* and *Arion subfuscus* takes place out in the open on the surface of the ground after dark, the peaks being soon

after the peaks of seasonal activity; the former species also mates to some extent throughout the year, whereas in the latter species mating is restricted to July–October. *Arion hortensis* and *ater* usually require some shelter, e.g. dead leaves, under which to mate, while it is presumed that the *Milax* species usually mate underground or under cover.

Section 10. By weighing the slugs species by species en masse as collected and then calculating the weight per 100 individuals, regular changes in weight throughout the year have been found. This method has been found to be as satisfactory for assessing seasonal changes in weight as the half-hour method of collecting slugs is for measuring seasonal changes in activity numbers. The slugs are heaviest soon after the greatest numbers are found active and at the time when the peak of mating occurs.

Section 11. The distribution of the species varies from garden to garden. *Arion hortensis* and *Milax gracilis* are most abundant in the gardens at the bottom of an old river bed slope and decrease steadily until their lowest numbers occur half-way up it. *Milax sowerbyi* has a ridge of abundance across the slope. *Arion subfuscus* is almost completely absent on the east side of the valley. Two particular gardens form the focal point of abundance of *Limax maximus*, and *Arion ater* is more abundant in gardens of recent origin in close proximity to coarse grass areas than in old well-established gardens. These distributions have persisted month by month throughout 2 years.

Section 12. There is some evidence that each species has its own regular curve of nightly activity, providing of course weather conditions are suitable. In the summer activity appears to be more closely adjusted to the time of sunset than in the winter. Immature specimens of *Arion hortensis* preponderated in steadily decreasing numbers in twilight collections made from May to December.

Section 13. All species are fully active at about 40° F., but some activity continues until almost freezing point; below this there is no activity. Some species, e.g. *Milax gracilis*, resume activity after cold spells later than others, e.g. *Agriolimax reticulatus*, perhaps owing to their deeper penetration of the soil.

Lack of surface moisture seems to be one of the factors limiting activity. Slug activity in rainless periods is reduced more at some periods of the year than at others. Rainless periods in the spring have less effect on limiting activity than summer droughts. This is probably due to the different water contents of the soil at these seasons. Activity is reduced while heavy rain is actually falling and also in heavy wind.

The optimum conditions for slug activity may be summarized thus: a warm still night with plenty of surface moisture either in the shape of recent rain or dew.

EXPLANATION OF PLATES 3–5

Miss Evelyn M. Tuke, Lecturer in Biology, Goldsmiths' College, University of London, has most generously painted eight of the common species of slugs found during this study at Harpenden. They include most of those of economic importance found in this country. In order to be able to compare the three species of *Milax* (see Part 1, § 2), Miss Tuke also painted some specimens, unfortunately not full grown, of *M. gagates* which Mr D. C. Thomas sent us from Devon.

Owing to the generosity of Messrs H. R. Napp, Ltd., the manufacturers of metaldehyde, to whom we express our grateful thanks for having shown their interest in scientific research in this most practical way, it has been possible to reproduce these paintings as three coloured plates. They are intended to supplement the key for the identification of the species (Part 1, pp. 144–5) and illustrate the characters used in their recognition. It is scarcely necessary to state that it is not claimed that the colours portray the extent of variation that occurs in slugs throughout the country, but they are faithful representations of the species as found by us most commonly in Harpenden. The length of each scale represents 1 cm. The copyright for the reproduction of these plates belongs to the authors and Miss Tuke.

ERRATUM, PART 1

P. 141, § 2, para. 2: *for* (? *carvanae* Poll.) (p. 145)
read (? *caruanae* Poll.) (p. 175)

Arion circumscriptus

Arion subfuscus
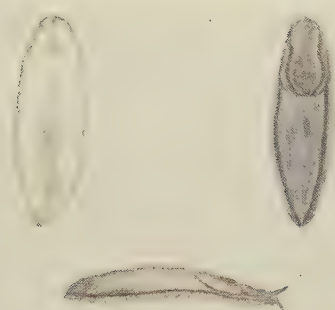
Arion hortensis
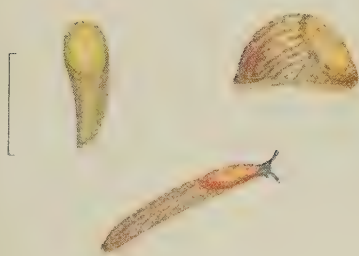
Arion ater, young
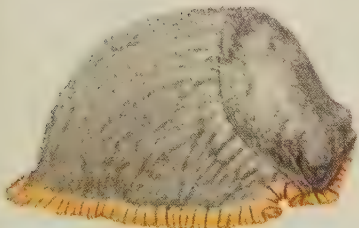
Arion ater

Arion ater

Evelyn M Tuke
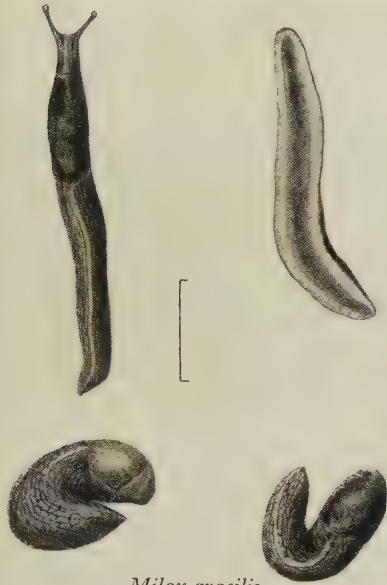
Milax gracilis

Milax gagates

Milax sowerbyi

Agriolimax reticulatus

Evelyn M. Tuke

Limax maximus

Evelyn M. Tuke

APPENDIX I. *Collections of active slugs in the back garden of No. 5 Moreton End Lane, Harpenden, after dark, 1941–3*

(In 1941 the collections made on 16 Oct., 9 and 10 Dec. lasted 60 min., while that on 23 Dec. went on for 45 min. The figures of the number of slugs obtained on these dates have been adjusted so as to be comparable with all the other entries, i.e. 30 min. collections.)

No. of slugs obtained in 30 min.

Date	Time of collection G.M.T.	Arion ater	Arion circumscriptus	Arion hortensis	Arion subfuscus	Milax gracilis	Milax sowerbyi	Agriolimax reticulatus	Limax flavus	Limax maximus	Total
1941: Sept.	—	1	0	0	24	12	3	155	0	0	195
16 Oct.	—	0	0	30	7	30	2	44	0	1	114
10 Nov.	—	0	0	40	9	26	3	53	0	0	131
11 Nov.	—	1	0	34	25	32	4	37	0	0	133
9 Dec.	—	2	2	44	11	11	2	34	0	1	107
10 Dec.	23.20–00.20	2	0	44	16	22	2	24	0	0	110
22 Dec.	20.30–21.00	6	3	64	6	21	5	30	0	0	135
23 Dec.	21.25–22.10	7	3	52	6	14	2	23	0	0	107
1942: 2 Jan.	20.15–20.45	5	4	84	14	37	4	32	0	1	181
24 Jan.	20.20–20.50	3	0	0	9	0	0	19	0	0	31
4 Mar.	18.45–19.15	0	0	10	6	1	0	15	0	0	32
11 Mar.	19.45–20.15	5	0	34	4	2	0	15	0	0	60
13 Mar.	20.25–20.55	0	1	42	4	4	1	4	0	0	56
14 Mar.	21.15–21.45	3	0	99	20	35	4	20	0	1	182
15 Mar.	19.30–20.00	2	2	106	19	28	6	24	0	0	187
29 Mar.	22.10–22.40	3	0	103	20	23	4	23	0	0	176
12 Apr.	19.55–20.25	5	0	86	47	34	7	51	0	0	230
13 Apr.	3.00– 3.30	1	0	84	26	12	0	11	0	1	135
24 Apr.	20.45–21.15	0	0	18	12	4	1	21	0	0	56
7 May	21.30–22.00	0	0	15	20	22	4	22	0	0	83
11 May	21.05–21.35	2	0	83	58	71	4	39	0	1	258
24 May	21.40–22.10	9	2	101	65	47	5	51	0	1	281
4 June	22.05–22.35	6	2	34	66	63	7	61	0	4	243
30 June	22.15–22.45	3	1	2	34	33	2	28	0	0	103
6 July	22.15–22.45	4	3	9	31	63	7	23	0	0	140
10 July	22.20–22.50	1	1	27	43	65	4	52	0	0	193
27 July	21.45–22.15	2	0	35	58	39	8	69	0	1	212
2 Aug.	21.40–22.10	5	0	61	73	67	9	91	0	2	308
4 Aug.	21.35–22.05	0	0	113	48	73	18	75	0	0	327
14 Aug.	22.35–23.05	5	0	76	62	87	21	103	0	0	354
21 Aug.	22.10–22.40	1	0	61	45	58	22	117	0	0	304
23 Aug.	21.00–21.30	1	0	83	26	86	12	105	0	0	313
31 Aug.	21.20–21.50	1	0	93	37	74	30	131	0	0	366
20 Sept.	20.35–21.05	1	0	84	26	79	22	138	0	1	351
28 Sept.	22.00–22.30	1	0	135	18	82	14	78	0	1	329
29 Sept.	21.10–21.40	0	1	141	19	97	9	67	0	0	334
30 Sept.	20.45–21.15	3	1	239	25	125	16	83	0	0	492
11 Oct.	20.50–21.20	1	1	165	26	86	23	81	0	0	383
17 Oct.	19.15–19.45	1	0	177	17	139	16	63	0	0	413
25 Oct.	19.15–19.45	0	2	208	15	54	10	67	0	0	356
28 Oct.	21.20–21.50	1	0	190	18	92	11	39	0	0	351
3 Nov.	19.10–19.40	3	0	215	24	99	8	33	0	0	382
15 Nov.	19.15–19.45	0	2	168	17	81	7	40	0	0	315
25 Nov.	19.05–19.35	1	0	131	9	80	5	34	0	0	260
25 Nov.	22.00–22.30	0	1	135	9	89	5	25	0	0	264
5 Dec.	21.30–22.00	2	0	102	13	32	5	22	0	0	176
6 Dec.	20.05–20.35	2	1	183	13	95	7	28	0	0	329
12 Dec.	19.15–19.45	1	0	201	10	54	5	38	0	0	309
13 Dec.	17.30–18.00	1	2	221	32	83	11	38	0	0	388
21 Dec.	18.15–18.45	2	2	229	20	78	8	43	0	0	382
1943: 12 Jan.	21.50–22.20	1	1	151	14	70	14	25	0	0	276
16 Jan.	19.30–20.00	2	1	131	28	45	2	29	0	0	238
19 Jan.	21.15–21.45	3	0	122	20	78	5	21	0	0	249

APPENDIX 1. *Collections of active slugs in the back garden of No. 5 Moreton End Lane, Harpenden, after dark, 1941–3*

(In 1941 the collections made on 16 Oct., 9 and 10 Dec. lasted 60 min., while that on 23 Dec. went on for 45 min. The figures of the number of slugs obtained on these dates have been adjusted so as to be comparable with all the other entries, i.e. 30 min. collections.)

No. of slugs obtained in 30 min.

Date	Time of collection G.M.T.	Arion ater	Arion circumscriptus	Arion hortensis	Arion subfuscus	Milax gracilis	Milax sowerbyi	Agriolimax reticulatus	Limax flavus	Limax maximus	Total
1941: Sept.	—	1	0	0	24	12	3	155	0	0	195
16 Oct.	—	0	0	30	7	30	2	44	0	1	114
10 Nov.	—	0	0	40	9	26	3	53	0	0	131
11 Nov.	—	1	0	34	25	32	4	37	0	0	133
9 Dec.	—	2	2	44	11	11	2	34	0	1	107
10 Dec.	23.20–00.20	2	0	44	16	22	2	24	0	0	110
22 Dec.	20.30–21.00	6	3	64	6	21	5	30	0	0	135
23 Dec.	21.25–22.10	7	3	52	6	14	2	23	0	0	107
1942: 2 Jan.	20.15–20.45	5	4	84	14	37	4	32	0	1	181
24 Jan.	20.20–20.50	3	0	0	9	0	0	19	0	0	31
4 Mar.	18.45–19.15	0	0	10	6	1	0	15	0	0	32
11 Mar.	19.45–20.15	5	0	34	4	2	0	15	0	0	60
13 Mar.	20.25–20.55	0	1	42	4	4	1	4	0	0	56
14 Mar.	21.15–21.45	3	0	99	20	35	4	20	0	1	182
15 Mar.	19.30–20.00	2	2	106	19	28	6	24	0	0	187
29 Mar.	22.10–22.40	3	0	103	20	23	4	23	0	0	176
12 Apr.	19.55–20.25	5	0	86	47	34	7	51	0	0	230
13 Apr.	3.00– 3.30	1	0	84	26	12	0	11	0	1	135
24 Apr.	20.45–21.15	0	0	18	12	4	1	21	0	0	56
7 May	21.30–22.00	0	0	15	20	22	4	22	0	0	83
11 May	21.05–21.35	2	0	83	58	71	4	39	0	1	258
24 May	21.40–22.10	9	2	101	65	47	5	51	0	1	281
4 June	22.05–22.35	6	2	34	66	63	7	61	0	4	243
30 June	22.15–22.45	3	1	2	34	33	2	28	0	0	103
6 July	22.15–22.45	4	3	9	31	63	7	23	0	0	140
10 July	22.20–22.50	1	1	27	43	65	4	52	0	0	193
27 July	21.45–22.15	2	0	35	58	39	8	69	0	1	212
2 Aug.	21.40–22.10	5	0	61	73	67	9	91	0	2	308
4 Aug.	21.35–22.05	0	0	113	48	73	18	75	0	0	327
14 Aug.	22.35–23.05	5	0	76	62	87	21	103	0	0	354
21 Aug.	22.10–22.40	1	0	61	45	58	22	117	0	0	304
23 Aug.	21.00–21.30	1	0	83	26	86	12	105	0	0	313
31 Aug.	21.20–21.50	1	0	93	37	74	30	131	0	0	366
20 Sept.	20.35–21.05	1	0	84	26	79	22	138	0	1	351
28 Sept.	22.00–22.30	1	0	135	18	82	14	78	0	1	329
29 Sept.	21.10–21.40	0	1	141	19	97	9	67	0	0	334
30 Sept.	20.45–21.15	3	1	239	25	125	16	83	0	0	492
11 Oct.	20.50–21.20	1	1	165	26	86	23	81	0	0	383
17 Oct.	19.15–19.45	1	0	177	17	139	16	63	0	0	413
25 Oct.	19.15–19.45	0	2	208	15	54	10	67	0	0	356
28 Oct.	21.20–21.50	1	0	190	18	92	11	39	0	0	351
3 Nov.	19.10–19.40	3	0	215	24	99	8	33	0	0	382
15 Nov.	19.15–19.45	0	2	168	17	81	7	40	0	0	315
25 Nov.	19.05–19.35	1	0	131	9	80	5	34	0	0	260
25 Nov.	22.00–22.30	0	1	135	9	89	5	25	0	0	264
5 Dec.	21.30–22.00	2	0	102	13	32	5	22	0	0	176
6 Dec.	20.05–20.35	2	1	183	13	95	7	28	0	0	329
12 Dec.	19.15–19.45	1	0	201	10	54	5	38	0	0	309
13 Dec.	17.30–18.00	1	2	221	32	83	11	38	0	0	388
21 Dec.	18.15–18.45	2	2	229	20	78	8	43	0	0	382
1943: 12 Jan.	21.50–22.20	1	1	151	14	70	14	25	0	0	276
16 Jan.	19.30–20.00	2	1	131	28	45	2	29	0	0	238
19 Jan.	21.15–21.45	3	0	122	20	78	5	21	0	0	249

Slugs in gardens

APPENDIX I (continued)

No. of slugs obtained in 30 min.

Date	Time of collection G.M.T.	Arion ater	Arion circum-scriptus	Arion hor-tensis	Arion sub-fuscus	Milax gracilis	Milax sower-byi	Agrio-limax reticu-latus	Limax flavus	Limax maxi-mus	Total
21 Jan.	20.20–20.50	0	2	118	10	73	5	25	0	0	233
28 Jan.	19.15–19.45	0	7	192	32	48	7	46	0	0	332
2 Feb.	19.45–20.15	1	0	128	45	36	2	28	0	0	240
20 Feb.	21.00–21.30	5	2	130	29	84	7	32	0	0	289
21 Feb.	19.30–20.00	5	1	96	18	45	5	40	0	0	210
23 Feb.	20.50–21.20	2	1	65	13	19	0	26	0	1	127
25 Feb.	21.20–21.50	1	1	144	29	64	0	21	0	1	261
6 Mar.	20.35–21.05	3	1	123	42	78	10	29	0	2	288
8 Mar.	20.20–20.50	1	0	72	23	10	4	23	0	0	133
18 Mar.	19.30–20.00	2	2	32	10	25	3	24	0	0	98
23 Mar.	20.30–21.00	3	2	78	29	48	11	24	0	0	195
29 Mar.	20.30–21.00	9	0	198	26	89	7	39	0	2	370
9 Apr.	20.45–21.15	4	3	119	47	89	7	36	0	0	305
13 Apr.	21.15–21.45	6	1	80	38	76	10	24	0	0	235
18 Apr.	21.30–22.00	3	0	17	30	34	3	12	0	1	100
23 Apr.	22.05–22.35	3	0	75	47	107	8	23	0	1	264
27 Apr.	21.40–22.10	5	0	115	87	102	11	28	0	0	348
5 May	22.05–22.35	3	1	67	81	87	8	28	0	1	276
13 May	21.45–22.15	3	1	62	84	102	15	28	0	1	296
22 May	21.30–22.00	3	1	43	108	109	9	28	0	1	302
26 May	22.15–22.45	6	1	101	112	155	15	22	0	0	412
30 May	22.20–22.50	9	0	21	129	91	8	34	0	2	294
6 June	22.30–23.00	1	1	60	99	110	8	21	0	0	300
13 June	22.20–22.50	5	0	14	112	84	14	62	0	1	292
21 June	22.45–23.15	2	0	8	106	84	12	87	0	1	300
24 June	22.35–23.05	3	0	6	101	59	4	75	0	5	253
28 June	22.45–23.15	4	0	2	71	55	6	59	0	1	198
3 July	22.30–23.00	1	1	1	42	26	7	74	0	1	153
11 July	22.30–23.00	2	2	4	88	79	5	87	0	2	269
16 July	22.30–23.00	1	0	6	61	42	7	98	0	0	215
20 July	22.15–22.45	0	0	3	41	42	9	53	0	2	150
24 July	23.00–23.30	3	1	28	71	101	17	125	0	0	346
1 Aug.	22.05–22.35	1	0	23	55	141	8	66	0	0	294
4 Aug.	21.50–22.20	1	0	17	35	81	15	119	0	1	269
7 Aug.	21.45–22.15	0	0	36	34	122	17	96	0	0	305
26 Aug.	21.10–21.40	0	0	46	28	129	17	79	0	0	299
28 Aug.	22.00–22.30	0	0	49	17	117	17	69	0	2	271
4 Sept.	21.35–22.05	0	0	60	27	73	16	47	0	0	223
10 Sept.	21.30–22.00	3	1	75	19	119	19	64	0	1	301
16 Sept.	21.35–22.05	0	0	73	27	166	27	62	0	0	355
21 Sept.	21.35–22.05	0	1	91	9	101	13	43	0	1	259
28 Sept.	21.45–22.15	0	0	140	16	293	25	29	0	0	503
5 Oct.	20.45–21.15	4	1	101	15	279	25	46	0	0	471
10 Oct.	21.00–21.30	0	2	137	9	371	17	34	0	0	570
10 Oct.	22.00–22.30	1	1	142	7	337	5	24	0	0	517
17 Oct.	19.10–19.40	0	6	210	8	237	14	30	0	2	507
23 Oct.	20.45–21.15	0	4	165	10	238	16	39	0	0	472
28 Oct.	20.15–20.45	2	1	203	8	275	15	55	0	0	559
2 Nov.	20.30–21.00	2	1	161	7	260	14	22	0	0	467
10 Nov.	19.15–19.45	0	0	122	12	101	12	49	0	0	296
21 Nov.	20.05–20.35	2	2	111	8	95	7	30	0	0	255
28 Nov.	19.25–19.55	1	1	105	9	124	9	24	0	0	273
7 Dec.	22.00–22.30	3	0	61	6	80	0	12	0	0	162
18 Dec.	22.15–22.45	0	0	96	8	129	2	19	0	0	254
25 Dec.	21.05–21.35	2	3	101	18	84	4	29	0	1	242

APPENDIX 2. *Collections of active slugs in other Harpenden gardens after dark, 1942–3*

(The gardens are arranged in alphabetical order of the roads; in addition the gardens on each side of the roads are kept together. The gardens are back gardens unless otherwise stated.)

Date	Time of collection G.M.T.	Arion ater	Arion circum-scriptus	Arion hor-tensis	Arion sub-fuscus	Milax gracilis	Milax sower-byi	Agrio-limax reticu-latus	Limax flavus	Limax maxi-mus	Total
				2 Clarence Road, north side							
1942: 6 Apr.	20.30–21.00	o	o	28	o	o	1	34	o	o	63
1943: 8 June	21.50–22.20	o	1	5	o	1	60	128	4	2	201
				4 Clarence Road							
9 June	22.20–22.50	o	o	3	o	2	8	95	o	3	111
				10 Clarence Road							
8 June	22.30–23.00	o	o	46	o	11	14	88	o	o	159
				7 Douglas Road, south side							
28 May	21.35–22.05	1	o	4	23	6	15	41	o	3	93
9 Oct.	20.40–21.10	o	o	37	4	9	7	43	o	1	101
				9 Douglas Road							
15 May	21.15–21.45	o	o	6	19	4	17	21	o	o	67
9 Oct.	21.20–21.50	o	o	67	2	25	13	99	o	o	206
				11 Douglas Road							
27 May	21.35–22.05	o	o	5	32	o	8	54	o	o	99
				13 Douglas Road							
28 May	22.15–22.45	o	o	2	5	1	1	71	o	o	80
				4 Douglas Road, north side							
11 May	21.45–22.15	o	17	171	24	135	6	39	o	o	392
12 Oct.	20.50–21.20	o	o	189	1	253	4	46	o	o	493
				6 Douglas Road							
28 Apr.	21.30–22.00	o	8	193	4	84	1	25	o	o	315
12 July	22.20–22.50	o	o	53	5	56	o	84	o	o	198
14 Sept.	22.50–23.20	o	o	195	2	57	3	52	o	o	309
				8 Douglas Road							
9 May	22.10–22.40	o	2	116	8	54	2	34	o	o	216
				10 Douglas Road							
1942: 8 Apr.	20.30–21.00	o	o	146	6	39	o	33	o	o	224
27 Apr.	20.50–21.20	o	o	4	1	2	5	25	o	o	37
19 May	21.30–22.00	o	1	99	7	44	4	34	o	o	189
16 July	22.10–22.40	1	o	45	17	23	2	69	o	o	157
10 Aug.	21.50–22.20	o	o	187	12	45	7	127	o	o	378
24 Sept.	20.10–20.40	o	o	234	12	55	11	146	o	o	458
5 Oct.	20.15–20.45	o	o	45	7	23	1	24	o	o	100
6 Oct.	20.15–20.45	o	o	268	5	73	12	79	o	o	437
25 Nov.	20.15–20.45	o	o	307	4	77	5	76	o	o	469
8 Dec.	19.00–19.30	o	o	305	5	97	4	64	o	o	475
1943: 13 Jan.	21.45–22.15	o	o	128	6	20	1	45	o	o	200
16 Jan.	20.15–20.45	o	o	219	8	25	1	52	o	o	305
28 Jan.	20.20–20.50	o	1	315	13	67	5	60	o	o	461
23 Feb.	19.20–19.50	o	o	114	2	22	o	59	o	o	197
24 Mar.	19.45–20.15	o	o	110	6	35	13	44	o	o	208
27 Apr.	21.00–21.30	o	1	192	36	85	4	48	o	1	367
26 May	21.35–22.05	o	1	157	29	57	16	77	o	o	337

APPENDIX 2 *(continued)*

No. of slugs obtained in 30 min.

Date	Time of collection G.M.T.	Arion ater	Arion circum-scriptus	Arion hor-tensis	Arion sub-fuscus	Milax gracilis	Milax sower-byi	Agrio-limax reticu-latus	Limax flavus	Limax maxi-mus	Total
				10 Douglas Road *(continued)*							
1943; 24 June	21.55–22.25	o	o	32	24	13	3	145	o	o	217
24 July	22.15–22.45	1	o	78	11	22	2	138	o	o	252
26 Aug.	22.10–22.40	o	o	152	7	45	8	98	o	o	310
28 Sept.	22.30–23.00	o	o	247	2	110	13	82	o	o	454
28 Oct.	19.30–20.00	o	o	225	2	87	6	33	o	o	353
27 Nov.	20.20–20.50	o	o	147	2	11	7	59	o	o	226
				12 Douglas Road							
10 May	22.15–22.45	o	1	134	7	36	7	10	o	o	195
				14 Douglas Road							
7 May	21.05–21.35	o	1	34	13	12	24	28	o	o	112
8 Oct.	20.45–21.15	o	o	130	1	36	31	87	o	o	285
				16 Douglas Road							
6 May	22.10–22.40	o	o	35	22	2	71	10	o	o	140
12 July	22.55–23.25	o	o	22	25	7	33	55	o	o	142
27 Aug.	22.30–23.00	o	o	51	6	31	100	65	o	o	253
1 Oct.	22.00–22.30	o	o	146	4	30	86	42	o	o	308
				18 Douglas Road							
11 May	21.10–21.40	o	o	21	29	2	42	17	o	1	112
13 Oct.	20.45–21.15	o	o	36	1	5	32	50	o	o	124
				20 Douglas Road							
10 May	21.30–22.00	2	1	75	11	26	6	27	o	1	149
				22 Douglas Road							
6 May	21.30–22.00	1	o	6	22	86	6	30	o	o	151
8 Oct.	21.25–21.55	o	1	70	2	205	8	68	o	o	354
		Luton Road, west side, Moreton End School									
21 June	22.10–22.40	1	2	6	109	37	4	72	o	1	232
13 Sept.	21.35–22.05	o	o	62	44	78	12	104	o	o	300
		Luton Road, Vane Lodge									
1942: 8 Apr.	21.10–21.40	3	o	120	5	12	1	13	o	o	154
27 Apr.	21.30–22.00	8	o	30	9	17	3	20	o	o	87
19 May	22.15–22.45	5	o	76	18	48	8	20	o	o	175
16 July	22.45–23.15	6	o	10	35	9	3	50	o	o	113
10 Aug.	22.30–23.00	9	o	81	35	22	23	159	o	o	329
24 Sept.	20.50–21.20	2	o	86	13	27	28	111	o	o	267
6 Oct.	20.55–21.25	1	o	127	9	45	23	84	o	o	289
26 Nov.	19.05–19.35	3	o	151	7	61	6	42	o	o	270
9 Dec.	20.35–21.05	4	o	130	13	56	7	33	o	o	243
1943: 29 May	22.15–22.45	5	o	28	38	39	21	31	o	o	162
		60 Luton Road, east side									
28 Apr.	20.55–21.25	o	1	30	o	2	22	28	o	o	83
12 Sept.	22.15–22.45	o	o	58	o	2	43	78	o	o	181
		62 Luton Road									
9 June	21.45–22.15	o	o	4	o	2	16	143	o	3	168
		64 Luton Road									
17 June	21.55–22.25	o	o	3	o	1	13	82	o	5	104
		66 Luton Road									
17 June	22.30–23.00	o	o	7	o	2	32	83	o	1	125
		68 Luton Road									
15 June	21.50–22.20	o	o	15	3	6	59	100	o	o	183

APPENDIX 2 (*continued*)

Date	Time of collection G.M.T.	Arion ater	Arion circum- scriptus	Arion hor- tensis	Arion sub- fuscus	Milax gracilis	Milax sower- byi	Agrio- limax reticu- latus	Limax flavus	Limax maxi- mus	Total
								No. of slugs obtained in 30 min.			
				70 Luton Road							
1943: 20 June	22.10–22.40	0	0	3	0	1	58	124	0	1	187
				72 Luton Road							
19 June	21.55–22.25	0	0	23	0	2	34	93	0	2	154
				74 Luton Road							
19 June	22.30–23.00	0	0	11	0	4	27	26	1	13	82
				76 Luton Road							
15 June	22.30–23.00	0	0	16	0	1	26	13	3	23	82
See Appendix 1			5 Moreton End Lane, back garden								
			7 Moreton End Lane, back garden								
1942: 2 Jan.	20.45–21.15	5	4	57	13	35	4	41	0	0	159
13 Mar.	21.10–21.40	2	1	32	5	9	0	16	0	0	65
12 Apr.	20.30–21.00	6	1	45	18	18	1	63	0	0	152
13 Apr.	3.30– 4.00	2	2	66	12	15	2	26	0	0	125
25 Apr.	20.30–21.00	2	1	30	21	11	3	78	0	0	146
11 May	21.45–22.15	9	4	65	27	48	8	95	0	7	263
4 June	22.40–23.10	6	3	13	38	23	4	93	0	1	181
12 July	22.10–22.40	3	1	8	30	21	2	52	0	1	118
28 July	22.10–22.40	2	0	13	29	17	5	73	0	0	139
7 Aug.	22.15–22.45	7	0	10	23	19	5	109	0	2	175
21 Sept.	20.05–20.35	4	0	50	22	79	20	126	0	0	301
12 Oct.	20.55–21.25	8	0	56	18	73	18	95	0	4	272
3 Nov.	20.20–20.50	3	0	105	5	58	13	44	0	0	228
6 Dec.	20.40–21.10	3	0	164	10	56	7	39	0	0	279
1943: 18 Jan.	18.45–19.15	3	0	55	16	17	0	63	0	1	155
31 Jan.	19.30–20.00	9	0	83	26	41	1	64	0	0	224
25 Feb.	20.05–20.35	7	0	72	20	45	11	71	0	0	226
24 Mar.	20.30–21.00	12	2	82	15	61	11	45	0	2	230
24 Apr.	20.45–21.15	5	0	54	31	31	7	52	0	1	181
25 May	21.30–22.00	13	1	34	73	39	15	46	0	1	222
27 June	22.00–22.30	3	0	5	39	27	0	145	0	1	220
23 July	21.55–22.25	11	0	3	37	25	3	145	0	2	226
27 Aug.	21.10–21.40	6	0	6	11	13	11	54	0	0	101
27 Sept.	22.00–22.30	0	0	38	1	39	6	42	0	1	127
25 Oct.	19.15–19.45	0	0	65	2	102	7	38	0	0	214
28 Nov.	18.30–19.00	2	1	44	8	66	2	36	0	0	159
			9 Moreton End Lane, back garden								
1942: 4 Jan.	18.30–19.00	34	6	25	23	5	10	45	0	2	150
14 Mar.	19.50–20.20	18	0	25	20	2	2	28	0	0	95
26 Apr.	20.50–21.20	8	0	2	17	0	9	46	0	0	82
12 May	22.00–22.30	24	1	12	33	6	13	68	0	1	158
12 July	22.40–23.10	6	0	0	27	1	14	12	0	3	63
11 Aug.	22.10–22.40	8	0	7	38	3	34	44	0	0	134
21 Sept.	20.50–21.20	6	0	20	29	13	100	112	0	0	280
1 Oct.	21.15–21.45	3	1	56	12	34	83	74	0	3	266
14 Oct.	20.55–21.25	5	1	64	13	37	91	75	0	1	287
4 Nov.	20.40–21.10	6	1	82	19	10	14	49	0	0	181
20 Nov.	22.20–22.50	5	0	95	13	40	26	28	0	0	207
6 Dec.	21.20–21.50	8	1	109	12	33	33	32	0	0	228
1943: 17 Jan.	19.15–19.45	10	0	54	6	9	4	22	0	0	105
29 Jan.	19.05–19.35	25	1	58	15	12	13	45	0	0	169
22 Feb.	19.25–19.55	6	0	18	4	5	4	34	0	0	71
19 Mar.	21.15–21.45	13	0	16	9	9	5	22	0	1	75

APPENDIX 2 (*continued*)

No. of slugs obtained in 30 min.

Date	Time of collection G.M.T.	Arion ater	Arion circum- scriptus	Arion hor- tensis	Arion sub- fuscus	Milax gracilis	Milax sower- byi	Agrio- limax reticu- latus	Limax flavus	Limax maxi- mus	Total
				9 Moreton End Lane, back garden (*continued*)							
1943: 3 Apr.	20.10–20.40	19	4	60	25	14	31	26	0	1	180
8 May	21.05–21.35	20	0	22	46	5	25	22	0	4	144
6 June	22.10–22.40	17	1	5	47	3	21	50	0	2	146
10 July	22.00–22.30	14	0	0	32	0	18	110	0	0	174
5 Aug.	21.50–22.20	7	0	3	34	3	25	118	0	1	191
8 Sept.	21.30–22.00	7	0	2	16	7	36	97	0	0	165
7 Oct.	21.45–22.15	3	0	82	7	33	38	74	0	2	239
4 Nov.	19.25–19.55	2	0	81	3	40	27	37	0	0	190
26 Dec.	18.20–18.50	4	1	47	3	44	15	25	0	1	140
				11 Moreton End Lane, back garden							
1942: 7 Apr.	20.10–20.40	10	0	12	24	5	3	92	0	0	146
26 Apr.	21.30–22.00	4	0	0	12	0	1	50	0	0	67
13 May	21.40–22.10	5	1	6	39	7	0	67	0	0	125
13 July	22.15–22.45	3	0	1	44	1	0	12	0	0	61
11 Aug.	22.40–23.10	1	0	0	63	1	12	90	0	0	167
23 Sept.	21.45–22.15	3	0	1	36	11	19	165	0	0	235
30 Sept.	21.30–22.00	1	0	14	19	21	38	106	0	1	200
15 Oct.	20.50–21.20	6	0	11	39	17	19	94	0	0	186
5 Nov.	21.00–21.30	0	2	48	18	26	20	45	0	0	159
7 Dec.	21.00–21.30	1	0	37	24	32	20	43	0	0	157
1943: 18 Jan.	19.25–19.55	1	0	12	29	3	3	21	0	0	69
31 Jan.	18.55–19.25	2	0	33	55	15	11	38	0	0	154
25 Feb.	20.45–21.15	0	1	10	18	14	4	22	0	0	69
30 Mar.	21.00–21.30	1	0	7	12	5	4	18	0	0	47
25 Apr.	20.50–21.20	6	0	4	26	14	7	14	0	1	72
25 May	22.05–22.35	7	0	2	25	2	4	36	0	0	76
27 June	22.40–23.10	6	0	0	48	0	6	163	0	1	224
23 July	22.35–23.05	3	0	1	41	2	3	73	0	2	125
27 Aug.	21.45–22.15	2	0	2	24	5	15	61	0	0	109
1 Oct.	21.15–21.45	0	0	5	18	20	34	74	0	1	152
25 Oct.	20.25–20.55	2	0	21	10	20	17	75	0	1	146
28 Nov.	22.05–22.35	3	0	15	2	8	5	19	0	0	52
				13 Moreton End Lane, back garden							
1942: 18 Mar.	20.55–21.25	13	0	9	26	7	0	74	0	0	129
13 Apr.	20.10–20.40	10	0	6	33	3	0	65	0	0	117
13 May	21.05–21.35	11	2	3	25	4	0	42	0	0	87
12 June	22.45–23.15	18	0	2	56	2	0	26	0	0	104
15 July	22.45–23.15	4	0	0	31	0	0	27	0	0	62
12 Aug.	22.55–23.25	17	0	0	34	0	0	47	0	1	99
22 Sept.	21.00–21.30	13	0	0	21	1	0	81	0	0	116
15 Oct.	20.10–20.40	12	0	9	19	5	0	56	0	0	101
6 Nov.	18.50–19.20	14	0	19	15	6	2	53	0	0	109
7 Dec.	20.25–20.55	2	0	22	20	21	1	46	0	0	112
1943: 13 May	21.10–21.40	8	0	3	50	4	2	24	0	0	91
18 Oct.	20.35–21.05	4	0	17	2	20	1	36	0	0	80
				15 Moreton End Lane, back garden							
1942: 4 Jan.	19.10–19.40	66	7	3	20	9	2	45	0	0	152
14 Mar.	20.30–21.00	28	0	4	20	4	0	39	0	1	96
13 Apr.	20.45–21.15	21	0	2	24	3	0	77	0	1	128
12 May	21.25–21.55	35	0	2	23	4	0	39	0	1	104
12 June	22.10–22.40	13	0	1	54	0	0	53	0	2	123
15 July	22.10–22.40	12	0	0	33	0	0	31	0	0	76
12 Aug.	22.20–22.50	23	0	0	55	1	0	45	0	5	129
22 Sept.	22.20–22.50	30	0	1	39	0	0	58	0	2	130
14 Oct.	20.15–20.45	37	0	4	19	6	1	50	0	3	120
6 Nov.	19.25–19.55	40	0	18	27	2	0	42	0	1	130
7 Dec.	19.15–19.45	13	1	22	32	14	0	34	0	0	116
22 Dec.	20.30–21.00	37	1	22	27	2	0	12	0	0	101

APPENDIX 2 (*continued*)

No. of slugs obtained in 30 min.

Date	Time of collection G.M.T.	Arion ater	Arion circumscriptus	Arion hortensis	Arion subfuscus	Milax gracilis	Milax sowerbyi	Agriolimax reticulatus	Limax flavus	Limax maximus	Total
				15 Moreton End Lane, back garden (*continued*)							
1943: 17 Jan.	21.00–21.30	32	1	12	31	11	0	52	0	0	139
29 Jan.	19.40–20.10	67	2	28	40	9	2	58	0	3	209
22 Feb.	20.25–20.55	10	0	4	8	4	0	22	0	0	48
19 Mar.	20.20–20.50	36	0	3	26	1	0	39	0	2	107
3 Apr.	20.45–21.15	69	1	16	62	5	2	40	0	1	196
8 May	21.40–22.10	34	1	9	50	6	1	13	0	5	119
6 June	21.35–22.05	102	2	3	110	4	0	19	0	1	241
10 July	22.35–23.05	34	0	0	58	0	0	15	0	3	110
5 Aug.	22.30–23.00	20	0	0	43	0	1	55	0	1	120
8 Sept.	22.05–22.35	13	0	1	20	0	1	87	0	0	122
7 Oct.	22.40–23.10	8	0	13	16	6	0	40	0	0	83
11 Nov.	20.30–21.00	17	2	23	28	6	3	41	0	0	120
26 Dec.	19.00–19.30	20	0	27	31	10	1	41	0	0	130
				17 Moreton End Lane, back garden							
1942: 22 Oct.	20.20–20.50	5	0	35	14	9	0	59	0	2	124
7 Nov.	18.55–19.25	3	0	51	9	2	0	45	0	1	111
				19 Moreton End Lane, back garden							
20 Oct.	20.15–20.45	7	0	30	15	17	0	38	0	0	107
22 Oct.	19.15–19.45	7	0	30	11	48	1	60	0	0	157
				21 Moreton End Lane, back garden							
29 Oct.	19.15–19.45	1	3	123	5	38	3	92	0	0	265
7 Nov.	20.15–20.45	1	0	87	10	21	3	73	0	0	195
9 Dec.	19.15–19.45	0	0	80	5	31	1	54	0	0	171
1943: 18 Oct.	19.10–19.40	0	0	107	6	39	0	61	0	0	213
				29 Moreton End Lane, back garden							
15 Oct.	20.30–21.00	0	0	46	5	3	22	37	0	0	113
				33 Moreton End Lane, back garden							
16 Oct.	20.30–21.00	4	0	60	18	42	17	82	0	0	223
			37 Moreton End Lane, back and front gardens								
6 Oct.	22.00–22.30	1	0	12	0	13	4	15	0	1	46
12 Oct.	21.45–22.15	0	0	5	2	27	5	14	0	0	53
			41 Moreton End Lane, back and front gardens								
14 Oct.	21.10–21.40	0	0	4	1	3	4	8	0	0	20
				47 Moreton End Lane, back garden							
15 Oct.	21.10–21.40	2	2	33	0	4	0	18	0	0	59
				5 Moreton End Lane, front garden							
1942: 9 Apr.	21.15–21.45	3	4	87	31	27	2	32	0	0	186
21 July	22.15–22.45	1	2	20	29	21	2	67	0	0	142
7 Aug.	22.50–23.20	1	3	46	20	65	5	72	0	0	212
28 Sept.	20.30–21.00	0	0	88	11	52	4	67	0	0	222
16 Oct.	20.45–21.15	0	0	114	16	97	2	60	0	0	289
15 Nov.	18.40–19.10	5	5	84	9	70	5	57	0	0	235
13 Dec.	19.25–19.55	4	5	121	18	82	1	57	0	0	288
				7 Moreton End Lane, front garden							
10 Apr.	20.10–20.40	6	3	87	23	30	2	51	0	0	202
21 July	22.50–23.20	2	1	3	25	0	0	44	0	1	76
8 Aug.	21.40–22.10	4	0	14	35	13	1	86	0	0	153
28 Sept.	21.10–21.40	3	0	35	12	23	3	56	0	0	132
17 Oct.	20.30–21.00	6	0	43	13	24	7	60	1	1	155
13 Dec.	20.25–20.55	4	0	68	12	21	13	44	0	0	162
				9 Moreton End Lane, front garden							
13 Oct.	19.20–19.50	0	0	6	6	5	10	90	0	0	117
14 Dec.	19.15–19.45	0	0	43	4	9	3	43	0	0	102

APPENDIX 2 (*continued*)

No. of slugs obtained in 30 min.

Date	Time of collection G.M.T.	Arion ater	Arion circumscriptus	Arion hortensis	Arion subfuscus	Milax gracilis	Milax sowerbyi	Agriolimax reticulatus	Limax flavus	Limax maximus	Total
				11 Moreton End Lane, front garden							
1942: 10 Apr.	20.45–21.15	2	o	56	5	8	o	67	o	2	140
22 July	22.30–23.00	o	o	1	16	o	o	17	o	o	34
8 Aug.	22.10–22.40	2	o	10	16	3	o	57	o	o	88
19 Oct.	19.20–19.50	3	o	23	13	7	7	109	o	o	162
14 Dec.	20.45–21.15	o	o	104	7	17	o	33	o	o	161
				13 Moreton End Lane, front garden							
11 Apr.	19.55–20.25	14	o	11	18	7	o	72	o	o	122
23 July	23.00–23.30	2	o	o	29	2	o	60	o	o	93
13 Aug.	22.00–22.30	2	o	2	15	o	o	92	o	o	111
19 Oct.	20.20–20.50	8	1	4	12	10	2	80	o	1	118
15 Dec.	19.10–19.40	6	o	32	15	10	2	38	o	o	103
				15 Moreton End Lane, front garden							
11 Apr.	20.30–21.00	29	4	21	19	8	o	67	o	o	148
23 July	22.20–22.50	4	o	o	31	1	o	43	o	o	79
13 Aug.	21.25–21.55	2	o	o	27	o	o	74	o	o	103
18 Oct.	20.20–20.50	12	o	6	10	13	1	62	o	o	104
15 Dec.	20.30–21.00	16	2	23	12	14	o	36	o	o	103
				3 Moreton Place, south side							
1943: 1 May	21.05–21.35	10	o	113	32	61	28	14	o	2	260
				5 Moreton Place							
12 May	22.00–22.30	35	o	32	52	11	63	62	o	4	259
6 Oct.	22.40–23.10	8	o	88	6	57	71	85	o	o	315
				7 Moreton Place							
12 May	21.25–21.55	10	o	6	56	1	17	22	o	2	114
				4 Moreton Place, north side							
29 May	21.35–22.05	15	2	28	103	25	4	25	1	6	209
				6 Moreton Place							
1 May	21.50–22.20	18	7	51	40	28	12	37	o	1	194
5 Oct.	21.30–22.00	1	o	80	6	53	40	58	o	o	238
				43 Ox Lane, north side							
13 July	22.10–22.40	o	o	1	o	o	1	21	o	o	23
11 Oct.	21.20–21.50	o	1	138	o	45	1	12	o	o	197
				47 Ox Lane							
13 July	22.50–23.20	o	o	1	4	1	o	14	o	o	20
11 Oct.	22.30–23.00	o	o	58	o	28	2	22	o	o	110
				Langdale, Salisbury Avenue							
1942: 14 Apr.	21.00–21.30	1	1	28	1	12	o	46	o	o	89
				23 Station Road							
4 Apr.	21.05–21.35	o	o	110	o	3	o	6	o	o	119
19 July	22.10–22.40	o	o	15	o	o	o	10	o	1	26
				Brookfield, Townsend Lane							
3 Jan.	23.00–23.30	4	6	28	1	3	o	11	o	o	53
3 Apr.	23.34–29.00	o	o	53	2	4	o	14	o	o	73
25 Apr.	22.30–23.00	o	o	5	2	2	o	17	o	o	26
14 May	22.20–22.50	6	1	34	13	o	o	36	o	1	91
11 July	22.30–23.00	o	1	3	12	o	o	27	o	o	43
9 Aug.	22.30–23.00	o	o	2	8	o	o	61	o	o	71
26 Sept.	22.15–22.45	o	o	11	1	o	o	37	o	1	50
16 Oct.	23.00–23.30	1	o	61	o	3	1	30	o	o	96
26 Nov.	22.30–23.00	o	1	82	o	4	o	15	o	o	102
12 Dec.	00.05–00.35	o	1	84	1	3	o	19	o	o	108

APPENDIX 3. *Collections of active slugs in places other than gardens after dark, 1942*

(The collection made on 15 Mar. at Crouch Hall lasted 60 min., the figures for this collection have been adjusted so as to be comparable with all the other entries, i.e. 30 min. collections.)

No. of slugs obtained in 30 min.

Date	Time of collection G.M.T.	Arion ater	Arion circum- scriptus	Arion hor- tensis	Arion sub- fuscus	Milax gracilis	Milax sower- byi	Agrio- limax reticu- latus	Limax flavus	Limax maxi- mus	Total
				Vegetable patch at 22 Douglas Road							
16 Mar.	21.15–21.45	0	0	51	2	36	0	7	0	0	96
				Vegetable patch at 24 Douglas Road							
19 Dec.	20.40–21.10	0	0	196	1	144	1	27	0	0	369
20 Dec.	21.05–21.35	0	0	175	2	66	1	25	0	0	269
21 Dec.	20.20–20.50	2	0	302	0	130	2	19	0	0	455
				Vegetable patch at Director's House, West Common							
17 Mar.	21.10–21.40	0	5	105	0	29	0	9	0	0	148
				Vegetable patch at 14 The Pleasance							
30 Mar.	20.30–21.00	0	0	66	5	193	5	44	0	0	313
30 Mar.	21.30–22.00	0	0	41	4	142	0	18	0	0	205
28 Apr.	20.45–21.15	0	0	0	1	5	0	5	0	0	11
15 May	21.15–21.45	0	1	34	11	173	1	33	0	0	253
22 May	21.45–22.15	0	0	50	4	253	1	19	0	0	327
				Crouch Hall, Redbourn (collections made by J. W. Weil)							
15 Mar.	19.30–20.30	1	0	33	1	0	0	18	0	0	53
18 Mar.	19.15–19.45	1	0	75	0	0	0	33	0	2	111
12 Apr.	—	2	0	18	0	0	0	57	0	0	77
				Potato patch at 5 Moreton End Lane							
9 June	22.10–22.25	0	0	3	6	8	0	3	0	0	20*
28 July	21.30–22.00	0	0	25	11	39	0	13	0	0	88
4 Sept.	22.45–23.15	0	1	48	18	130	12	43	0	0	252
6 Sept.	22.00–22.30	0	0	28	4	71	6	13	0	0	122
13 Oct.	20.30–21.00	1	3	44	8	33	2	32	0	0	123
20 Oct.	20.50–21.20	0	1	37	4	57	1	6	0	0	106
8 Dec.	22.00–22.30	0	0	56	12	102	10	41	0	1	222
				Allotment 1							
17 Mar.	20.35–21.05	0	6	51	0	12	0	161	0	0	230
				Allotment 2							
31 Mar.	20.00–20.30	3	0	24	0	2	0	185	0	0	214
				Allotment 3							
31 Mar.	20.35–21.05	0	0	57	0	18	0	73	0	0	148
				Field: Harpenden potato club, pre-planting							
7 Apr.	21.00–21.30	0	0	1	1	0	0	40	0	0	42
				Glasshouse							
2 Apr.	21.40–22.10	0	0	1	0	2	0	11	0	0	14

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* Abandoned after 15 minutes

THE AGE AND GROWTH OF EELS (*ANGUILLA ANGUILLA*) FROM THE WINDERMERE CATCHMENT AREA*

PART 2

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(With 8 Figures in the Text)

CONTENTS (PART 2)

4. AGE OF YELLOW EELS

Satisfactory age determinations were obtained from 286 yellow eels. The age of the eel is recorded as years spent in fresh water, the previous sea life being ignored (p. 30), but it is the accepted practice to include in records of length and weight the 8·0 cm. and 0·4 g. attained by the fish before its entrance into fresh water.

(*a*) Age and length of yellow eels

The length of the 286 eels examined for age ranged from 9 to 95 cm. The sex for 185 was definitely female, and that of 7 male; of 44 fish where sex was not noted, 15 were, from their size, almost certainly female, and 29 could have been either male or female, the remaining 50 fish were too small for sex to be determined (p. 28). The eels are considered together irrespective of sex, although the results will clearly refer p redominantly to females.

The data obtained from the age determinations in relation to length are presented in two ways: (1) as an age for length relationship so that the mean age of a fish at a chosen length is given, (2) as a length for age

relationship so that the mean length attained by each year class is given. The first is regarded as the chief expression of the results, since it recognizes the fact that the age determinations are estimates, whereas the length data are certainties. The results thus expressed can also be used to obtain information about age when only length data are available. The second method of presentation is given since it is that usually employed in reports on eels, and thus the Windermere results may be compared with those from other waters. It must be noted that both methods strictly give a length and age relationship and not rate of growth, since back calculation has not been used in estimating the age.

(1) *Age for length of yellow eels*

The eels were divided into 3 cm. length groups of which the means ranged from 10 to 95 cm. The numbers of specimens in the groups below the 19 cm. and above 55 cm. was small; the other groups, except one, contained at least 10 fish. The mean age, the range and the standard deviation for each of the length groups are given in Table 4 and Fig. 7. In the figure two straight regression lines, which are the best-fitting straight lines to the means of age and length,

Table 4. *Age for length relationship of yellow eels. Mean age in years and its standard deviation and the range in years for each of the different 3 cm. length groups*

Length groups 3 cm. ...	10	13	16	19	22	25	28	31	34	37	40	43	46	49	52
Mean age in years	1·0	2·0	3·0	3·4	4·3	4·7	5·0	6·1	6·5	7·3	8·3	8·6	9·2	10·0	11·3
Range	0	0	2–4	2–4	3–5	4–6	4–6	5–8	5–9	5–9	7–10	7–10	7–11	9–12	10–13
Standard deviation	0	0	1·0	0·69	0·72	0·75	0·70	0·91	1·06	0·92	0·87	0·82	1·04	0·96	1·15
No. of specimens	1	3	5	10	15	19	13	7	17	26	29	34	25	14	22

Length groups 3 cm. ...	55	58	61	64	67	70	73	76	79	82	85	88	91	95
Mean age in years	11·4	11·0	12·0	13·0	13·0	14·0	14·0	14·0	14·6	14·7	15·7	—	17·0	17·0
Range	10–13	10–12	0	0	0	12–15	13–15	0	14–16	14–16	15–16	—	0	0
Standard deviation	1·08	1·0	0	0	0	1·73	1·4	0	1·35	1·37	1·14	—	0	0
No. of specimens	14	5	1	2	1	3	2	2	6	4	4	—	1	1

are shown.* It was clear that a straight line represented the age for length relationship up to 11 years better than a curve, but also that the same line did not fit the older year groups at all well, therefore two lines, one from 19 to 58 cm. and the other from 61 to 95 cm., were fitted. The importance of this and the fact that there is a significant difference between the regression coefficients for the lines (on applying the 't' test a value of P less than 0·01 was obtained) are discussed later (p. 115).

(2) Length for age of yellow eels

The mean length for each year group, the range in length and the standard deviation are given in Table 5 and Fig. 8; in the figure twice the standard deviation is presented, so that approximately 95 % of the observations will fall within it. The means given in Tables 4 and 5 indicate that in general the growth of the yellow eel is slow, although the high value of some of the standard deviations shows that more rapid growth may occur (and of course slower growth too). The marked difference between the length attained by the XIII and XIV groups suggesting a change in growth rate at this point may be the result, though not necessarily so, of sampling methods.

In Table 6 the only other data on the growth of eels in British waters are given, namely, those for the

* The lines were fitted to the weighted means by the method of least squares under the direction of Mr H. J. Buchanan-Wollaston. The equation for the lower group of means was $7·8 + 0·6844 \dfrac{(x-39·1)}{3}$ and for the upper $14·5 + 0·4533 \dfrac{(x-74·44)}{3}$ The line through the lower means when tested by the Z test gave a value of P less than 0·05, showing that there is a slight but significant deviation from straightness but no indication of a systematic deviation from straightness. The upper line gave a value of P greater than 0·05, showing no significant deviation from straightness.
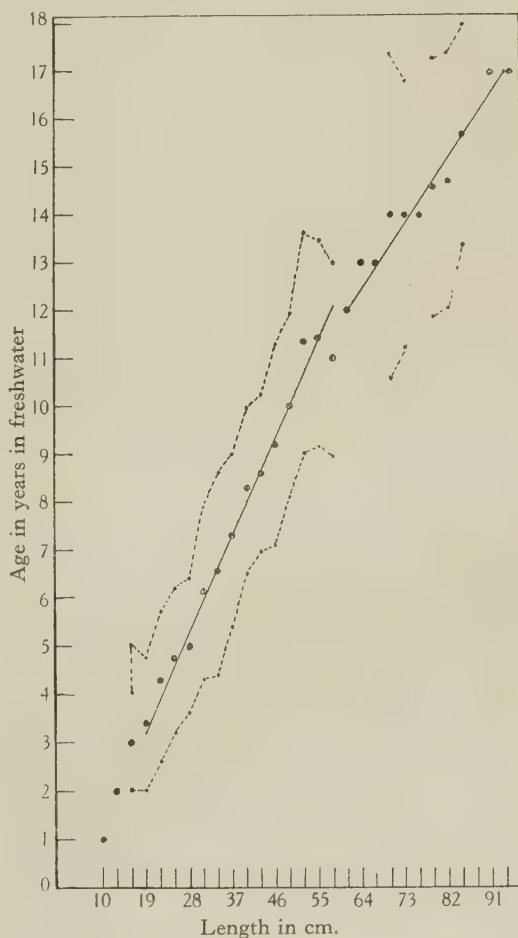
Fig. 7. Age for length relationship of yellow eels. The mean age for each 3 cm. length group and twice its standard deviation; the regression lines fitted to the means, one from 19 to 58 cm. and the other from 61 to 95 cm., are shown.

Table 5. *Length for age relationship of yellow eels. Mean length and its standard deviation and the range in cm. for the different age groups: mean length in inches also noted*

Age group ...	I	II	III	IV	V	VI	VII	VIII	IX
Mean length in cm.	9·0	15·4	19·5	22·7	26·4	32·2	38·4	40·8	43·2
Range in cm.	0	12–19	16–22	15–28	21–36	25–37	32–45	32–47	34–50
Standard deviation	0	2·61	1·87	3·40	3·48	3·67	3·27	3·28	3·22
Mean length in in.	3·5	6·0	7·6	8·9	10·3	12·6	15·1	16·0	17·0
No. of specimens	1	6	7	25	24	25	22	41	42

Age group ...	...	X	XI	XII	XIII	XIV	XV	XVI	XVII
Mean length in cm.		48·6	51·8	55·9	57·9	79·9	76·7	83·0	93·0
Range in cm.		39–59	45–58	50–70	51–73	75–82	69–84	80–86	91–95
Standard deviation		4·84	3·55	5·08	7·15	2·57	6·19	2·45	2·83
Mean length in in.		19·1	20·3	22·0	22·7	31·4	30·1	32·6	36·6
No. of specimens		30	17	14	11	7	7	5	2
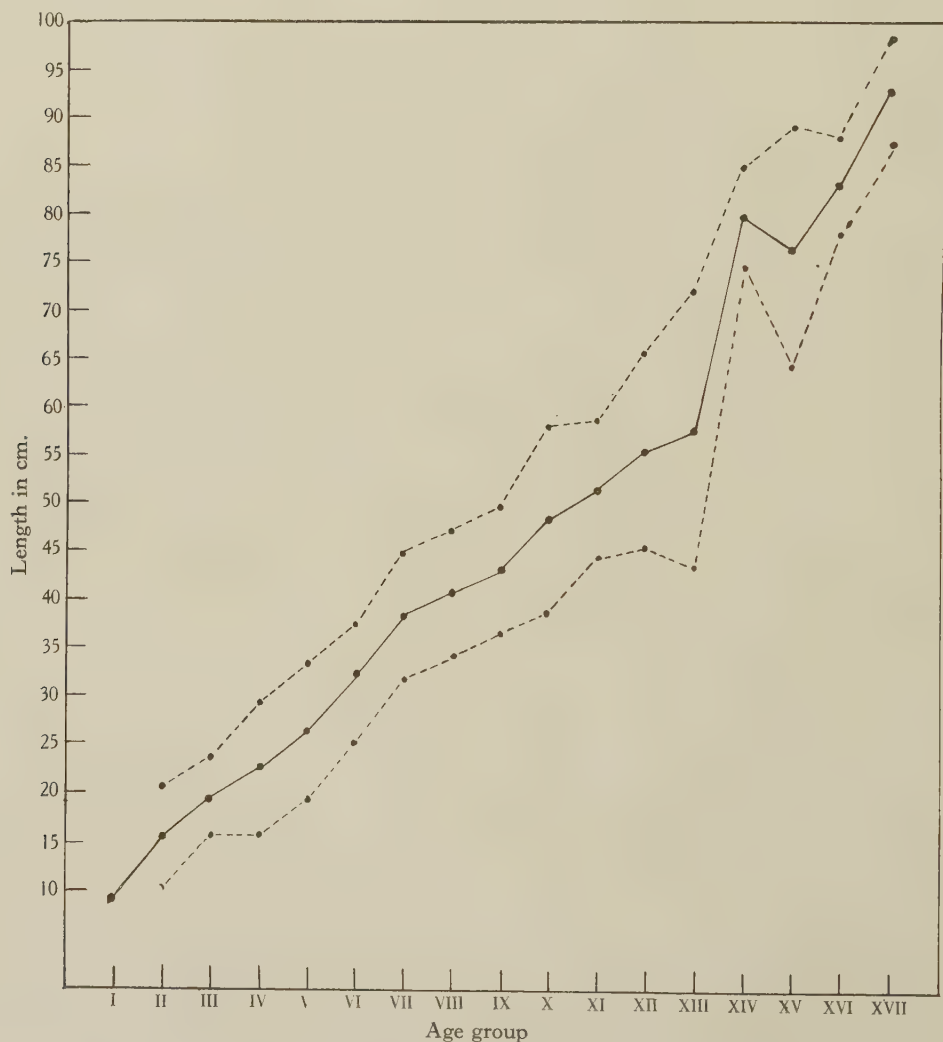
Fig. 8. Length for age relationship of yellow eels. The mean length for each age group and twice its standard deviation.

River Severn and the River Clare or Clare-Galway (in Ireland) of Marcus (1919) and for a Worcestershire pond (Hornyold, 1922).

Marcus's (1919) study of Severn eels was based on 152 fish captured near Epney. He points out that the Severn eels and those of the Lower Elbe and Alster (the data presumably from Ehrenbaum & Marukawa, 1913) grow at an almost uniform rate up to IV group, but that following this the Severn eels rapidly fall behind the German ones. He attributes the slower growth in the Severn to the fact that this river opening towards the Atlantic receives enormous quantities of elvers which result in the river being over-populated with eels, too many for the available food supply. He remarks that the struggle for food is proved by the fact that cannibalism frequently occurs; unfortunately, he gives no data in support of this statement.

group, but the Windermere fish have made appreciably better growth afterwards, the Irish specimens in the upper groups are, however, very few in number.

Hornyold (1922) determined the age of 78 eels from a Worcestershire pond, 46 females and 30 males and two whose sex was indeterminate. His results (Table 6), most likely affected by the inadequacy of his material, show that these eels made poor growth compared with the Windermere specimens.

(b) Age and weight of yellow eels

Eels of 1000 g. and less were weighed in grams and heavier specimens in pounds and ounces which were converted to grams (1 oz. = 28·35 g.). Of the 286 eels examined for age 271 were weighed as well

Table 6. *The length in cm. for age of yellow eels in other British waters; figures in italics represent male and female data when combined. Marcus group I is comparable with Windermere II and so on*

Body of water	sex	Age group														
---	---	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
Windermere		9·0	15·4	19·5	22·7	26·4	*32·2*	38·4	40·8	*43·2*	48·6	51·8	55·9	57·9	79·9	76·7
R. Severn (Marcus, 1919)	♂	13·5 (1)	13·5 (1)	17·5 (2)	24·7 (5)	27·0 (26)	28·3 (40)	32·1 (42)	33·8 (6)	38·5 (1)						
	♀					26·9 (5)	28·5 (7)	32·1 (7)	36·6 (7)	45·5 (1)	54·5 (1)					
						27·0	*28·3*	*32·1*	*35·5*	*42·0*						
Clare River, Ireland (Marcus, 1919)	♂					35·5 (1)	33·5 (2)	34·1 (5)	34·9 (5)	35·3 (4)	37·8 (3)	39·5 (2)				
	♀				33·5 (1)	32·6 (9)	35·6 (38)	38·5 (53)	41·0 (44)	41·7 (18)	41·5 (4)	43·5 (3)				
						32·9	*35·2*	*38·1*	*40·4*	*40·5*	*39·9*	*41·9*				
Worcestershire pond (Hornyold, 1922)	♂					21·0 (1)		31·0 (2)	30·3 (14)	31·7 (12)	36·0 (1)	40·0 (1)				
	♀							33·5 (4)	34·6 (7)	34·4 (13)	40·5 (4)	41·3 (7)	44·0 (5)	44·5 (4)	48·0 (1)	48·0 (1)
								32·7	*31·5*	*33·1*	*39·6*	*41·2*				

Remembering that Marcus's group I must be compared with Windermere group II, comparison of the Severn and Windermere data shows that the Windermere fish have a greater length for age in all the age groups; this applies whether the results are those given for the Severn females or the male and female, or for all fish from this river. It may be that the Windermere drainage area is not overstocked as compared with the Severn; certainly the run of elvers up the River Leven, the outflow from Windermere, is but a fraction of the run up the Severn. Marcus (1919) investigated the growth of eels taken from one other water in the British Isles, an Irish river which he could not name with certainty but which he postulates as likely to be the Clare River (Clare-Galway) which flows into Lough Corrib. He examined 192 fish, of which 170 were females (Table 6). Reading Marcus's group I as comparable with Windermere group II and so on, it is seen that the English eels have much the same length for age relationship as the Irish ones until the VII year

as measured. These fish ranged in weight from 1 to 1785 g. and were predominantly female. Eels of the same age may differ widely in their weights, and a mean for any age group, unless based on many data, may be misleading. Some indication, however, of the relationship between age and weight may be gained from the means based on the 271 observations available. Weight may be calculated from length from the expression giving the length-weight relationship (p. 120) and in Table 7, mean weights for each year class so calculated are given. These means are probably a more reliable index of the age-weight relationship than the observed means, since length-weight considerations were based on a fair number of eels.

Eels grow in weight very slowly, the average fish being nine or ten years in fresh water before reaching a weight of ½ lb. (226 g.), and even in the older groups, where it appears that the annual increase in weight is greater than in younger fish, a fish does not achieve 3 lb. until it reaches the XV group. Walter (1910)

notes that Hübner found that a yellow eel became 2½ lb. (pfund) in weight in 15 years, and that a similar result was obtained by Strück.

5.   AGE OF SILVER EELS

It has already been stated that the silver eels came from three traps, one situated on the Cunsey Beck and the other two on the River Leven (p. 28). The great majority of the fish came from the Cunsey trap and thus do not represent the silver eels of Windermere, the lake from which the yellow eels were taken, but of Esthwaite Water (see Fig. 1, p. 27). It is most unlikely that in comparing the age of the yellow and silver eels this fact is significant. Of the 275 individuals giving satisfactory age determinations, 240 were female and 35 were male. The females, which ranged from 47 to 97 cm. in length and from 210 to 2040 g. in weight, will be considered first.

From consideration of the means and range of both Tables 8 and 9 it appears that silver eels of less than 70 cm. gain little in length by spending a longer time in fresh water, but this would not seem to apply to those above this length. This contains the suggestion that the larger eels have arisen from yellow eels which have had more rapid growth, a point which is considered later (p. 115). The tables show that in general the eels became silver after having spent 10½–12½ years in fresh water by which time they are mostly 55–60 cm. in length. This deduction receives further evidence and its value is extended from consideration of Fig. 11.

In Fig. 11 a length-frequency curve of the silver eels taken at the trap at Cunsey Beck is given. It is based on the results of 1222 measurements made during the seasons 1939–44, but since various selective factors operated upon the catch during these years, the records for 1944, when such factors were

Table 7. *Yellow eels. Mean weight and range in weight, in g., for different age groups; calculated mean weight, computed from mean length of group (Table 5) given for each age*

Age group	I	II	III	IV	V	VI	VII	VIII	IX
Mean length of weighed specimens	9·0	15·4	19·5	22·7	26·4	32·3	38·4	40·7	43·9
Mean weight	1·0	5·4	11·3	17·2	28·4	51·5	96·0	107·0	131·0
Range in weight	0	3–9	5–19	6–31	14–60	26–115	57–180	70–180	90–240
No. of specimens	1	5	7	25	24	25	22	40	39
Calculated mean weight	—	5·0	10·7	18·0	29·1	52·8	86·7	110·7	132·0

Age group	X	XI	XII	XIII	XIV	XV	XVI	XVII
Mean length of weighed specimens	48·3	57·9	55·9	57·3	78·4	77·1	83·3	95·0
Mean weight	206·0	220·0	323·0	392·0	1013·0	1124·0	1285·0	1785·0
Range in weight	95–380	140–330	200–720	200–890	842–1303	540–1587	1134–1360	0
No. of specimens	29	15	14	10	5	6	3	1
Calculated mean weight	198·0	239·1	326·3	371·5	1057·3	1024·5	1336·0	—

(a)   Age and length of female silver eels

(1)   Age for length of female silver eels

The eels were divided into 3 cm. length groups, the means of which ranged from 46 to 96 cm. The number of specimens in the groups above 67 cm. is small. The mean age, its standard deviation and the range in years for each length group are given in Table 8 and Fig. 9; they show that the eels may have spent from 9 to 19 years in fresh water before migrating, with a mean migration age of 12·27 years. This mean may have been influenced by sampling methods, but probably not to any appreciable extent.

(2)   Length for age of female silver eels

The mean length in cm. attained by each age group, its standard deviation and the range in length for each group is given in Table 9 and Fig. 10. The method does not give a very satisfactory indication of the probable length achieved for any age; since the mean is much affected by the wide range in each group.

negligible, are given separately; they support the results obtained from the total data. Mr H. J. Buchanan-Wollaston analysed, visually, the frequency distribution into what he considered to be its likely components (dotted line in Fig. 11), and I interpreted them in terms of year groups basing the interpretation on the age and length results given in Tables 8 and 9.

In Fig. 11 it is apparent from the length-frequency curve that most of the female silver eels migrate when they are between 54 and 60 cm. long, and that the number migrating when they have attained a large size, which may be regarded as a length of over 70 cm., is small. (These facts in relation to the growth of the yellow eel are discussed later, p. 115.) Now, although it appears from the age-frequency curve in Fig. 11 that eels 54–60 cm. long are most likely to have spent 10, 11 and 12 years in fresh water, a point which receives some support from Tables 8 and 9, it is also evident from Tables 8 and 9 that eels of this length may have spent from 9 to 15 years in fresh water. Therefore it is suggested that length is the

factor, rather than age, which induces migration. This length in the Windermere catchment area is 54–60 cm.; if in other waters a different modal length for migration is found, it need not invalidate the suggestion that migration is dependent upon size and not age. It seems unlikely that length is of itself the factor responsible: probably it is only an index of some physiological condition associated with it.

The suggestion that migration depends on size and not age is of interest in view of some results obtained by Bellini (1907, 1910) from eels reared in experimental ponds at Comacchio. He found that on the average the females became silver after 4½ years when at a length of 55·1–66·3 cm. and after 6½–7 years at 79·0–90·6 cm.; the former thus migrate at the same length as the Windermere eels, but at a very different age.

determinations comparable with my Windermere data, this has been done and is noted in Table 10. Comparison of such data with those in Table 9 shows that Jespersen's fish, although coming from the same catchment area as my own, are much smaller for their age than mine, but it is difficult to assess the value of this distinction, since the methods used for the age determinations are not strictly similar.

(b) Age and weight of female silver eels

The mean weight and range in weight of the eels of different age groups is given in Table 11. The number of fish on which such means are based is only 123 of the 240 examined for age, since the weights of 84 specimens, being taken some time after death, could not be used. Therefore the calculated mean weight for each age group, computed from the mean

Table 8. *Age for length relationship of female silver eels. Mean age in years, its standard deviation and the range in years for each of different 3 cm. length groups*

Length group 3 cm. ...	46	49	52	55	58	61	64	67	70	73
Mean age in years	11·0	10·2	11·3	11·3	11·7	12·1	12·6	13·7	14·0	15·3
Range	0	9–12	9–14	9–14	9–15	10–15	10–15	11–15	13–15	14–17
Standard deviation	0	1·09	1·10	1·16	1·35	1·16	1·33	1·37	1·4	1·76
No. of specimens	1	13	32	38	61	31	27	10	2	3

Length group 3 cm. ...	76	79	82	85	88	91	94	97	All fish
Mean age in years	—	16·0	15·5	16·5	16·2	16·7	17·0	18·0	12·27
Range	—	15–17	15–16	15–19	15–19	16–17	0	17–19	9–19
Standard deviation	—	1·0	0	1·5	2·14	1·18	0	1·4	1·99
No. of specimens	—	3	2	6	4	4	1	2	240

The influence of length, as opposed to age as a factor governing seaward migration, has already been shown for salmon and sea-trout smolts. It was pointed out by Pentelow, Southgate & Bassindale (1933) that, in the River Tees, 'in general it is necessary for smolts to attain a physiological condition which is connected with a certain age before they migrate', and that this size was attained at different ages. Went (1938) found in connexion with the salmon of the River Shannon that 'the parr must attain some physiological condition associated, at least as an index, with the minimum size before smolt migration takes place' and shows how age is governed by this length requirement.

Reference may be made to the length for age results obtained by Jespersen (1926) based on 119 female eels sent to him from Newby Bridge in December 1920 and examined by him in Copenhagen: from the place and time of capture they were presumably silver eels. Otoliths were used to some extent to determine the age of these fish, but the determinations were 'mainly based on countings of the growth rings in the scales' and 'have therefore only a relative value'. In Table 10 Jespersen's data for the 'average length for the various year groups' are given. Since it is most likely that three pre-scale years should be added to his year groups (p. 33) to make his age
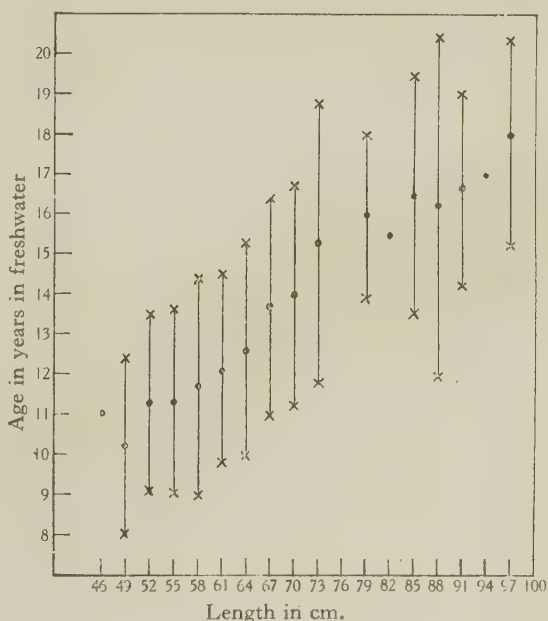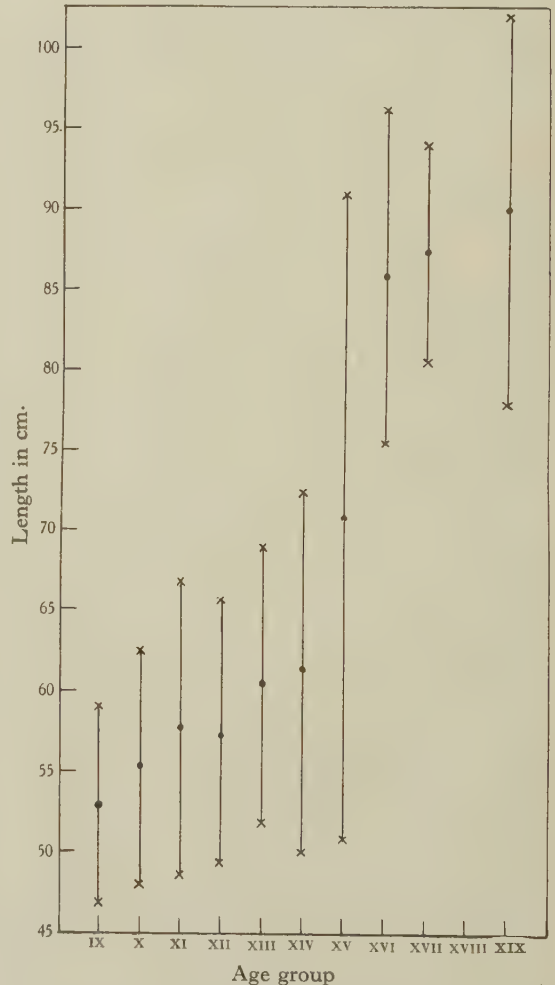

Fig. 9. Age for length relationship of female silver eels. The mean age for each 3 cm. length group; twice its standard deviation is indicated by crosses.

Table 9. *Length for age relationship of female silver eels. Mean length, its standard deviation and the range in cm. for the different age groups; mean length in inches also noted*

Age group ...	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XIX	All fish
Mean length in cm.	52·9	55·3	57·7	57·4	60·5	61·3	70·8	85·8	87·4	90·0	60·78
Range in cm.	49–57	48–63	47–66	49–66	52–70	53–74	58–87	79–92	72–96	86–97	47–97
Standard deviation	3·08	3·60	4·55	4·05	4·35	5·64	10·05	5·22	3·42	6·08	3·23
Mean length in in.	20·8	21·7	22·7	22·5	23·8	24·1	27·8	33·7	34·4	35·4	23·9
No. of specimens	9	29	59	54	40	13	19	5	9	3	240

length of the group and the expression obtained for the length-weight relationship of female silver eels (p. 120), is also given in Table 11. Comparison of the mean weights of the different age groups is difficult, since the range in weight in each group is so great. General consideration of both means and range shows that there is a gradual and appreciable increase in weight with each year up to the XIV group, in subsequent age groups the increase in weight for each year of added life appears to be much greater. The mean observed weight for all the female silver eels of the Windermere catchment is 556 g. (1 lb. 3 oz.); this is, however, affected by the high proportion of large fish included in the 123 observations, and therefore the mean weight computed from the mean length of all silvers (60·78 cm.) and the length-weight expression 410 g., is also noted.

Data from the eels taken at the trap on Cunsey Beck give further information on the age and weight relationship. It will be remembered that the Cunsey Beck drains only a part of the Windermere catchment. The mean weight of 365 female silver eels caught over a period of four years is 396 g. The mean length of the 1222 specimens from which Fig. 11 is based is 58 cm., which length, in terms of the age groups shown in that figure, would coincide with the XI year class, then on the reasonable assumption that the means for length and weight may be associated it is concluded that 396 g. is attained after 11 years spent in fresh water.

The weight for age relationship found in some continental waters may be noted. Ehrenbaum & Marukawa (1913) state that a silver eel of a pound (pfund) weight, measuring 64–66 cm., has usually spent 10–11 years in fresh water. Wundsch (1916), referring to this conclusion, remarks that of those waters which he studied which are 'favourable' to eels this weight is reached in 7 or 8 years. Lübbert (1928) notes that the work of Ehrenbaum, Marukawa and Marcus has shown that in favourable waters glass eels take 4–5 years, in less favourable ones 7–9 years, to reach a length of 50–60 cm. and with that a weight of ½–1 lb. Walter (1910) states that Strück, a German fish farmer, estimated that a silver eel of ¾–1½ lb. weight had been 4 years in fresh water, but adds that Strück did consider this age estimate as perhaps too

Fig. 10. Length for age relationship of female silver eels. The mean length for each age group; twice its standard deviation is indicated by crosses.

low. Information about the weight for age relationship of the silver eels from the famous eel farms at Comacchio seems to be limited to the data provided by results obtained from Bellini's experimental ponds

(1907, 1910). His figures show that those eels which were under normal conditions of food and environment of the lagoons achieved a mean weight of 190 g. (7 oz.) in 4½ years and 740 g. (1 lb. 11 oz.) in 7 years

(c) Age and length of male silver eels

Male silver eels seldom occurred in the trap at the Cunsey Beck; even of the 680 fish caught in 1943, the record catch, only 3 % were males. At the com-
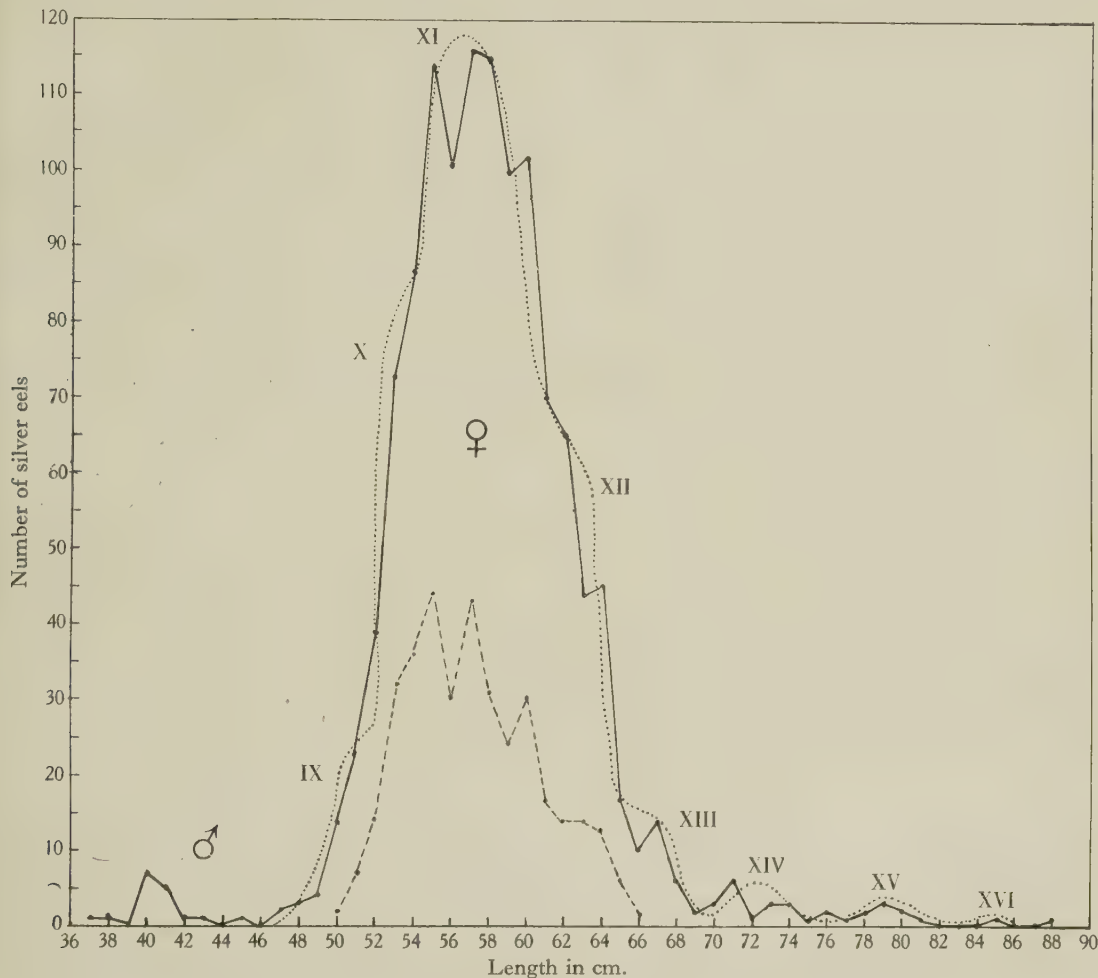
Fig. 11. Length-frequency curve of silver eels measured at Cunsey Beck trap, 1939–44; data for 1944 only shown by broken line. Analysis of curve into component year groups shown by dotted line.

Table 10. '*Average length for various year groups for eels from Newby Bridge*' (as recorded by Jespersen, Table III, 1926)

Data from Jespersen (1926)	No. of scale rings ...	VIII	IX	X	XI	XII	XIII	XIV	XV	XVII	XVIII
	No. of specimens ...	17	39	29	17	7	5	2	1	1	1
	Av. length in cm. ...	47·8	50·5	53·7	55·6	61·9	64·0	85·0	73·0	88·0	83·0
Year group if 3 pre-scale years added to number of scale rings		XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX

and those reared under five different types of environment when considered collectively ranged from 190 to 340 g. (7 oz. to ¾ lb.) for 4½ years and from 740 to 2115 g. (1 lb. 10 oz. to 4 lb. 10 oz.) for 6½ to 7 years.

mercial fisheries at Newby Bridge and Backbarrow the fishermen allege that 'small silvers' (fish which are therefore almost certainly males) always form a small proportion of the season's catch. Continental workers are of the opinion that, generally speaking,

male eels are more likely to be found in estuaries, their numbers declining and those of the females increasing with inland waters. This numerical relationship between male and female eels with which, apparently, an environmental factor is involved, raises problems concerning the fundamental cytological structure of the reproductive organ of the eel, the time when sex is determined and the effect of environment in determining it. These matters have received consideration from continental workers, whose results, however, it is not relevant to discuss here.

The 35 male silver eels examined were identified as of that sex by the scalloped reproductive organ accepted as the male gonad (p. 28). All the fish were measured; they ranged in length from 35 to 43 cm., and the 34 specimens weighed ranged from 65 to 150 g.; the age of all was determined.

the age of the migrants, from 7 to 12 years, but there is very little range, 35–43 cm., in their length.

(d) Age and weight of male silver eels

The mean weight for each age group is given in Table 14.

The length and weights characterizing the male and female silver eels present a marked contrast. During the investigation no male exceeding 43·0 cm. in length has been found, and although small females do occur, the smallest being a recent capture measuring 44·0 cm., such fish are most uncommon. The mean weight of the males, 112 g. (4 oz.), is greatly below that of the females (556 g., 396 g. and calculated 410 g.). This relative smallness and lightness of the male is not confined to the eels of the Windermere catchment, it characterizes the 'runs' of silver eels

Table 11. *Silver eels, females. Mean weight and range in weight, in g., for different age groups: calculated mean weights, computed from lengths in Table 9, also given*

Age group	IX	X	XI	XII	XIII	XIV
Mean length in cm. of weighed fish (no. in brackets)	53·8 (7)	55·8 (10)	55·8 (20)	57·6 (30)	60·8 (23)	60·1 (7)
Mean weight and range of weighed fish	279 230–330	338 190–425	340 220–525	353 225–562	414 290–674	405 330–610
Calculated mean weights	279·5	316·6	355·2	350·1	404·0	420·0

Age group	XV	XVI	XVII	XIX	All fish
Mean length in cm. of weighed fish (no. in brackets)	73·2 (11)	85·8 (3)	87·4 (9)	90·0 (3)	62·7 (123)
Mean weight and range of weighed fish	848 330–1587	1511 1360–1814	1611 670–2040	1672 1445–2040	556 190–2040
Calculated mean weights	624·8	—	—	—	410

(1) Age for length for male silver eels

The eels were divided in three 3 cm. length groups, and the mean age, standard deviation and range in years found (Table 12).

Table 12. *Age for length of male silver eels*

Length group 3 cm.	36	39	42	All fish
Mean age in years	8·0	9·2	9·4	9·06
Range	7–9	7–11	8–12	7–12
Standard deviation	0·89	1·24	1·21	1·43
No. of specimens	6	16	13	35

(2) Length for age of male silver eels

The age determinations expressed as a length for age relationship are given in Table 13.

Considering the two tables together it may be concluded that most male eels migrate after 8–11 years spent in fresh water when they are from 38 to 42 cm. long; the mean age at migration is after 9 years spent in fresh water when the length attained is practically 40 cm. There is an appreciable range in

from other lakes, such as Coniston Water and Ullswater, in the district, it has been noted on the silver eel fisheries of the River Bann, Northern Ireland, and on the Continent it is a well-established and long-recognized fact.

The mean age of the males at migration is appreciably lower than that of the females, 9·06 as opposed to 12·27 years. Thus the males are not only smaller but younger fish. It might be objected that the age of the male has been underestimated owing to the difficulties which attend age determinations. This, however, seems most unlikely, since the most reliable otoliths are those which give readings up to 8 or 9 years. Age determinations of Continental workers show that the male silver eel, as well as being smaller than the female, is also appreciably the younger fish. This characteristic of earlier maturity has been recorded for other species of fish. In Windermere the male perch matures a year before the female (Le Cren, unpublished data). In most waters it has been found that the male of the brown trout reaches sexual maturity before the female. Of marine fish, male hake, cod and plaice mature earlier than the female.

6. DISCUSSION ON THE AGE AND LENGTH RELATIONSHIP OF YELLOW AND SILVER EELS

The foregoing accounts of the age and length relationship found in yellow and in silver eels raises a question about the rate of growth of the yellow eels which involves some discussion concerning the age and length at silvering. The facts relevant to this discussion are presented in Figs. 11 and 12. The former has already been described. Fig. 12 shows the age for length relationship of each individual yellow and silver eel examined for age; it is a detailed exposition of the data upon which Figs. 7 and 9 are based; the two regression lines which fit the means of Fig. 7 are also shown. The discussion concerns all the yellow eels and the female silver eels.

Figs. 11 and 12 show that (a) the first silver eels occur at 46 cm., (b) the greatest number of silver eels are from about 55 to 60 cm. long, and that of these the majority have been 10–12 years in fresh water,

representation of age will be random; selection for length is unlikely to have operated among eels of over 75 cm. Although, therefore, the significance of the difference between the two regression coefficients may not be justified on the data available because of the comparative exclusion of fish of 60–75 cm., any effort to establish a relationship between the eels of less than 60 cm. and those of over 75 cm. by an exterpolation of the lower regression line is unsatisfactory. Thus it is on the assumption that the two regression coefficients are significantly different, with its implication that the large eels of the upper group have grown more rapidly than the smaller ones of the lower group, that the following remarks on the growth of the large eels are made.

It may be postulated that the population of eels in Windermere is composed of one type of eel only or that two types are present. Assuming that the population is composed of one type, this type will exhibit the normal variations in growth found among such fish populations. Then if silvering takes place first

Table 13. *Length for age of male silver eels*

Age group	VII	VIII	IX	X	XI	XII	All fish
Mean length in cm.	37·2	39·8	39·9	40·4	40·6	43·0	39·9 $\sigma = 1·97$
Range	36–38	37–42	35–41	39–43	38–43	—	35–43
No. of specimens	3	9	11	8	3	1	35

Table 14. *Weight, in grams, in relation to age of male silver eels*

Age group	VII	VIII	IX	X	XI	XII	All fish
Mean weight	94·0	114·9	105·5	121·9	119·0	120	112
Range	90–97	80–130	65–130	105–150	100–142	0	65–150
No. of specimens	3	9	10	8	3	1	34

and (c) that there are much larger eels but that these are few in number. Concerning the regression lines in Fig. 12, attention has already been directed to the fact that the regression line which fitted the age for length means below 11 years and 58 cm. did not fit the means above this age and length to which a separate line was fitted, and that the regression coefficients of these two lines were significantly different (p. 107). The facts and the position of lines in Fig. 12 imply that the larger eels are growing faster than the smaller ones. It will be noted that the upper regression line when exterpolated intersects the lower at 50 cm. and 9 years.

Here it must be mentioned that in the data shown in Fig. 12 there may have been some selection, for length, of the bigger eels which favoured those over 75 cm. against those from 60 to 75 cm. But the data in Fig. 11, which were practically unselected, show that the big eels, though few in number, are nevertheless more abundant than would be expected if they were merely the upper variation of the 55–60 cm. mode. Also in Fig. 12 any selection was purely for length, and therefore in any one length group the

among the smaller and slower growing yellow variants it will act as a selective factor and expose the larger and quicker growing individuals. In such a case the mean length of these larger yellow eels should be greater than that of the silver eels of the same age, but comparison of the data in Tables 5 and 9 show that, for the age groups IX–XIII, this is not so. Thus on the assumption of one type of eel, selection by silvering will not explain the presence of the large quick-growing eels in Fig. 12, an explanation of which may now be sought based on the assumption that the eel population contains two co-existent types of eel differing in their growth and time of silvering. The types are represented by the smaller slower growing majority and the few larger quicker growing individuals present in Fig. 12.

Two arguments may be based on this assumption: (1) that the large eels have throughout life grown more quickly than the smaller ones, (2) that all the eels have grown at the same rate up to a certain point, after which some of them adopted a more rapid growth and resulted in the large eels of Fig. 12; both arguments will be considered.
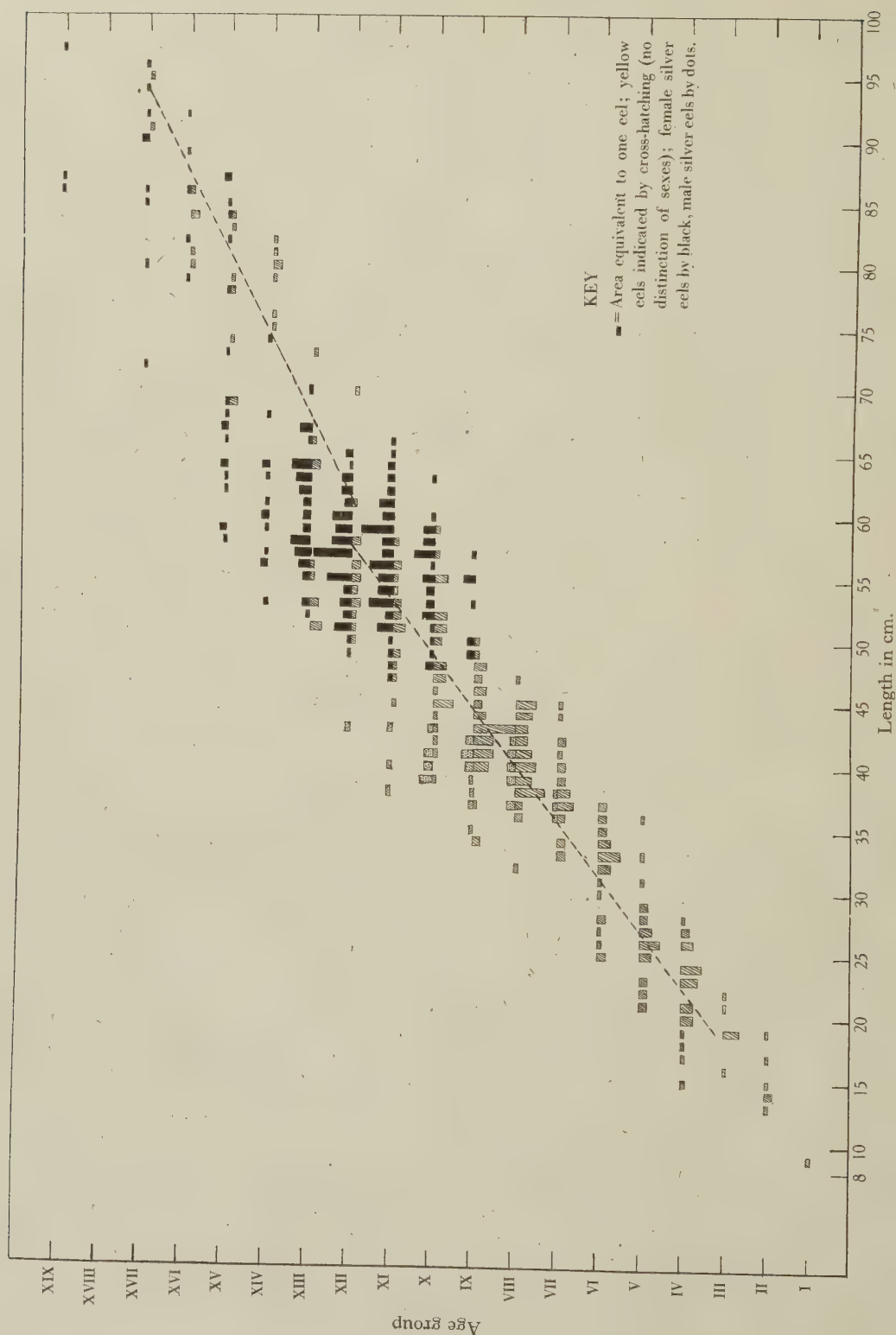
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KEY

■ = Area equivalent to one eel; yellow eels indicated by cross-hatching (no distinction of sexes); female silver eels by black, male silver eels by dots.

Fig. 12. The ength plotted against age for individual yellow and silver eels; regression lines for age-length relationship of yellow eels (Fig. 7) shown by broken line.

(1) We know that the large eels are few in number (Figs. 11 and 12), therefore their existence and their more rapid growth would be masked by the mass of the smaller and slower growing individuals until these latter are eliminated by becoming silver. It has, however, been pointed out under the postulate of one type of eel, that silvering, as it occurs among the general population, affects the larger eels first. When, however, it is postulated that there are two co-existent types of yellow eels it is possible as a result to maintain that there is a minority of eels which do not silver until later, these then being apparent as the few larger and old eels of Figs. 11 and 12. This argument of there being two types of eels which are distinguished by their different rates of growth, present throughout the life in fresh water, is of interest in view of Bellini's belief that the growth and final size of the adult eel is conditioned by the size of the elver (1907).

(2) The second argument, based on the assumption that there are two types of eel, supposes that all the yellow eels grow together until about 9 years and 50 cm., the earliest age and length for silvering, and, it will be noticed, the point of intersection of the two regression lines in Fig. 12. It is suggested that this time and length mark a critical point when some physiological change takes place which results in the eel either continuing to grow at the previous rate and becoming silver within the next few years or assuming a more rapid growth rate and delaying silvering until much larger and older. The few eels that follow the latter alternative are the large and old yellow and silver eels of Figs. 11 and 12.

Summarizing, therefore, the growth of the eels, it is found that there is a small minority of them which become silver when older and larger than the majority. It appears from the data available, the accuracy of which is a moot point, that this minority has a more rapid rate of growth than the majority which silver when younger and smaller. It is submitted that this more rapid rate may have been present throughout the whole of the life in fresh water but, alternatively, it may have been assumed at a certain age and length, implying an abrupt change; arguments for both have been given.

It has been noted (footnote, p. 27) that some investigators believe that there are two types of yellow eel, the broad headed and the narrow headed. Evidence based on morphometric data, growth-rate results and studies of feeding habits brought forward by Continental workers to distinguish the two is conflicting and inconclusive. Generalizing on the subject Ehrenbaum (1929) notes that the broad-headed (Breitkopf) grows to a larger size than the narrow-headed eel (Spitzkopf), the former is not under $1\frac{1}{2}$ lb. at migration, the latter not above $1\frac{1}{4}$ lb. Windermere eels were not distinguished into the two types, but Ehrenbaum's remark suggests that possibly the larger older eels were broad-headed.

7. LENGTH-WEIGHT RELATIONSHIP OF EELS

(a) Length-weight relationship of yellow and silver eels

The length-weight relationship of a fish expressed by the formula CW/L^3 may be expressed by $10^5W/L^3$ when there is no change in the shape and/or substance throughout life, and a length-weight coefficient (K) may be calculated from this formula. Such coefficients were determined for yellow eels of 9–95 cm., these fish consisting of specimens of which the sex was not yet apparent (p. 28) and those of which the sex was determined, they being predominantly female. When the values of K obtained were plotted individually against the length of the eel to which they applied they showed a tendency to rise with increasing length, the rise taking the form of a curve. Mr H. J. Buchanan-Wollaston, examining the data, suggested that a cubic regression line should be fitted to the weighted means of the values of K for eels of 13–85 cm. arranged in 3 cm. length groups. Under his direction three regression coefficients were found by the method of multiple regression and the curve in Fig. 13 drawn from the equation

$$Y = \bar{y} + b(x - \bar{x}) + b_2(x - \bar{x})^2 + b_3(x - \bar{x})^3$$

$$= 162 \cdot 76 + 2 \cdot 963 \frac{(x^2 - 40 \cdot 75)}{3} + 0 \cdot 110 \frac{(x - 40 \cdot 75)^2}{3}$$

$$+ 0 \cdot 0015 \frac{(x - 40 \cdot 75)^3}{3}.$$

Thus the yellow eel changes its shape as it increases in length, a change which, it may be deduced from the curve, involves the eel becoming more bulky and heavier in substance or both as it grows longer. When the data upon which Fig. 13 was based were plotted as log length against log weight for individual eels it was found that the points up to 33 cm. fitted a different line from that which took in the remaining points, indicating a point of discontinuity in the change of shape at approximately 33 cm.; such a discontinuity is not apparent in Fig. 13. It is of interest to speculate whether this discontinuity in the change in shape may underlie the differentiation of yellow eels into 'snigs' and ordinary yellow eels (p. 27), a distinction which, though in practice real enough, eludes definition.

The length-weight coefficients for female silver eels were also calculated from the formula $10^5W/L^3$. When the mean values of K for each centimetre length from 48 to 70 were plotted against the length to which they applied, they showed a slight tendency to fall with length, while the few remaining individual values, for eels above 70 cm., rose with length. A straight regression line fitted to the weighted

means of the values of K for eels of 48–68 cm. was drawn from the equation

$$Y = a + b(x - \bar{x}),$$

$$Y = 187 \cdot 18 + (0 \cdot 964 \times 10 \cdot 25).$$

This, when subjected to the 't' test, showed that the fall was statistically significant. Thus the silver eel also changes its shape with increasing* length, a change which, it may be deduced from the line in Fig. 13, means that in considering longer and longer eels bulk will be less and substance lighter or both. (In Fig. 13 the observed mean values of K for silver eels above 68 cm. are given, each mean being based on less than five specimens. These means fall into

be of interest, since comparison of the power of n for yellow and silver eels might throw some light on the relation between length-weight and silvering. Therefore it was decided (1) to determine whether this change could be represented in terms of L^n in which n is not equal to 3, and (2) to find if there was any significant difference in the value of the power of n for female yellow and female silver eels. These considerations were based on female silver eels of 45–70 cm., since by far the majority are of this length, and on all the available female yellow eels of this length range. A regression line, $\log W = c + n \log L$, was fitted by the method of least squares to the lengths and weights of 202 yellow eels and 302 silver
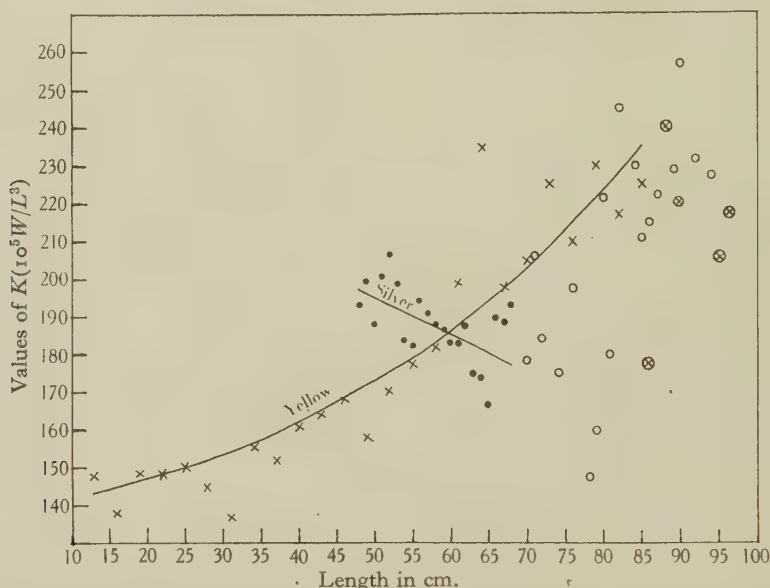
Fig. 13. Regression lines giving calculated mean values of K plotted against length for all yellow eels and for female silver eels. Observed means from which regression lines calculated shown by crosses for yellow and spots for silver eels. Observed means not included in calculation of the two lines shown by circles, plain for silver, crossed for yellow eels.

two groups of which only the lower one would show any agreement with the regression line, the upper departing from it appreciably. This departure suggests that the length-weight relationship in large silver eels is of a different order from that of the general population.)

Therefore, as shown by the two regression lines in Fig. 13, the shape and substance or both of all yellow eels and of female silver eels is influenced by the length of the eel, the effect of length in this respect being different in the yellow and silver eels.

This difference of effect suggested that a determination of the change in shape and substance or both of yellow and silver eels in terms of L^n would

* Since silver eels do not grow, 'increasing length' means the consideration of longer and longer specimens, not the increased length of an individual.

eels over a range of 45–70 cm.; the two lines are given in Fig. 14. From these lines the values of c and n in the equation $cW/L^n = 1$ were obtained so that length-weight coefficients, which for the average eel would be unity, could be calculated. The formula obtained for yellow eels (of between 45 and 70 cm.) was $3667 W/L^{3 \cdot 4709}$, and for silver eels of the same length $206 \cdot 6 W/L^{2 \cdot 7628}$.

When the difference between the value of the power of n for yellow and for silver eels was tested for significance, it was found that the value of P corresponding to the difference divided by its standard deviation was less than 1×10^{-6}; thus there is no doubt whatever that the slope of the regression lines for yellow and silver eels is really different. The difference between the position of the lines was tested by finding whether the means of the log

weights were significantly different. This gave a value of $d/\delta d$ of 2·025, being therefore equal to 0·043, proving that the position of the lines for yellow and silver eels is just significantly different.

The value of the power of n when tested was found to deviate significantly from the value of three both in yellow and in silver eels.

Thus the length-weight relationship in eels is established as deviating from the cube law and as being different for yellow and silver eels, this difference having been proved to be definitely significant. It must be remembered here that the yellow eels came from Windermere, whereas the silver eels, being caught at the trap on Cunsey Beck, were derived from the yellow eels of Esthwaite Water, and thus conceivably the difference might be attributed to this fact. On the assumption that this is not so it may be considered how this difference in the length-weight relationship of yellow and silver eels, demonstrated graphically by the slope and position of the lines in Fig. 14, may be interpreted in terms of the relationship between yellow and silver eels.

The fact presented by the graph is that the lines intersect at 58·06 cm. and at 361·4 g., and that below this intersection a silver female eel is heavier than a yellow female eel of the same length, above the intersection a silver eel is lighter than a yellow eel of the same length. Two interpretations of this phenomenon may be suggested:

(a) It may suggest that below 58·06 cm. the heavier yellow eels of each length become silver, above 58·06 cm. the lighter yellow eels of each length have become silver. Implicit in this is the idea that the transformation of a yellow eel into a silver eel is dependent on a particular combination of length and weight having been attained. This combination is achieved in eels of less than 58·06 cm. among those which are heavier for their length and in eels of above 58·06 cm. among those which are lighter for their length; 58·06 cm. and 361·4 g. presents the ideal or optimum length-weight relationship for silvering.

(b) Alternatively, the fact that a silver eel is heavier below and lighter above 58·06 cm. than a yellow eel of the same length may be taken as indicating that the transition from yellow to silver involves a change in the length and weight or both of the yellow eel. In this case if a yellow eel of less than 58·06 cm. becomes a silver eel of the same length there is a gain in weight, and if a yellow eel of more than 58·06 cm. becomes a silver eel of the same length there is a loss in weight; since, however, it is not known whether a yellow eel does become a silver eel of the same length, there are possibilities of various combinations of gain and loss or both in weight and in length (which will differ above and below 58·06 cm.) which will occur in the transition from yellow to silver.

Both (a) and (b) are presented as hypothetical interpretations of the facts presented by the slope and position of the two regression lines; of the two

(a) is the simpler. It may be noted in connexion with (a) that this interpretation might explain the existence of those few very large yellow and silver eels of which mention has already been made (p. 115). They may represent the result of an inability to
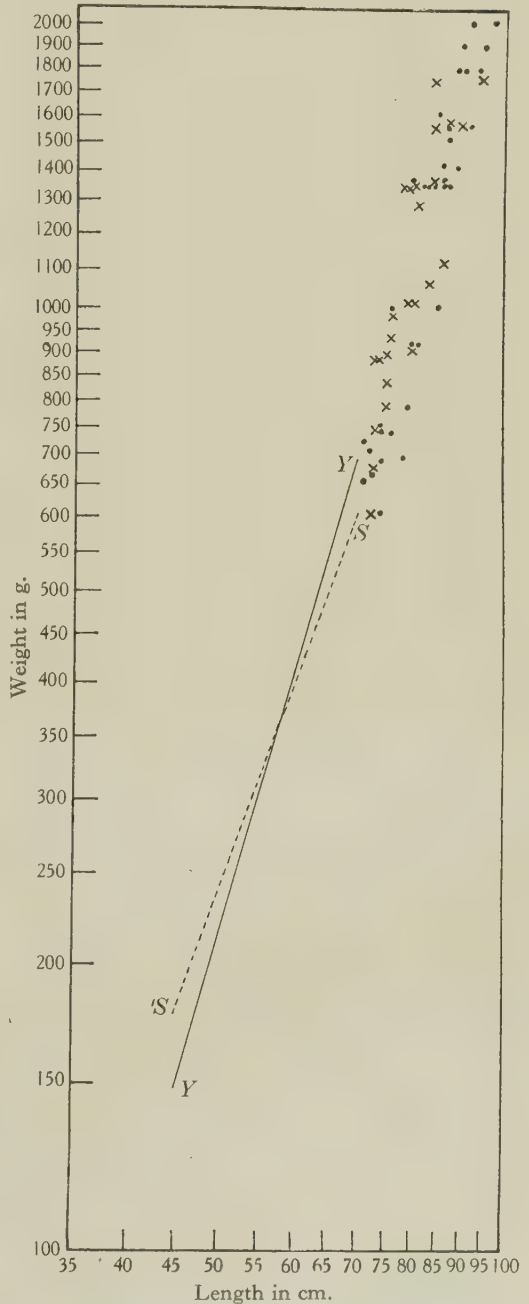

Fig. 14. Regression lines fitted to lengths and weights of yellow and silver female eels of 45–70 cm. Data for individual fish above 70 cm. also given.

achieve within the usual lengths and weights found for silver eels that particular combination of length and weight, the result of which is silvering; they have attained such a combination only when much longer and heavier than the average eel.

The yellow and silver eels represent two well-marked stages in the life history of the eel, and it is not surprising to find that they differ in length-weight relationship. The definitions of length-weight for female yellow and silver eels given above are, however, based on limited data and therefore cannot be regarded as conclusive. The interpretations of the definitions in terms of the relation of length-weight to silvering are thus of restricted value, primarily serving to indicate that this relation is complicated and, at present, obscure. It may be noted that the weights of fat, protein and mineral salts are different in yellow and silver eels (McCance, 1944); it is not possible, however, to relate this fact to the different length-weight relationship of yellows and silvers on our present inconclusive knowledge of the latter.

The length-weight relationship of male silver eels was not considered, since thirty-five fish provided too few measurements.

(b) *Observations based on length-weight coefficients*

In order to consider the effect of age, season and retention upon the length-weight relationship ('condition') of eels, length-weight coefficients were obtained. For yellow eels these were found by dividing the observed value of K ($K = 10^5 W/L^3$) for any length by the mean value of K for the same length, this mean value being obtained from the formula for the cubic regression line or read directly off the curve itself in Fig. 13; the resultant ratio being the length-weight coefficient ('condition factor'). For silver eels the coefficients were obtained by the same method, the mean values of K being in this case determined from the formula given for the straight regression line in Fig. 13 (p. 118) or read directly from the line itself. Length-weight coefficients so calculated were considered in regard to age, season and retention.

In both yellow and silver eels the length-weight coefficients showed no definite trend with age. Yellow eels, which were taken at all seasons of the year, were divided into bi-monthly captures of May–June, July–August, September–October and November–December, the number of specimens taken in each period being 100, 137, 100 and 26 respectively. The mean length-weight coefficient found for May–June was 0·97, for July–August 0·96, for September–October 1·06 and for November–December 1·13, indicating that the eels taken in the later part of the year had a higher length-weight relationship than those taken earlier in the season.

Some female silver eels, captured during the autumn, were retained in tanks in the laboratory or in floating boxes in the lake for 4–6 months. There was a definite impression that such eels had lost weight during their captivity; measurements indicated that there was no decrease in length. The length-weight coefficients of 97 of these kept eels, which ranged in length from 48 to 65 cm., were determined giving a mean value of 0·91, and confirming the usual impression of loss of weight with retention. Petersen (1894) remarks concerning kept eels that 'silver eels are wintered in reservoirs from September to October of one year until the April–May of the next, without losing more than a few per cent in weight during that time'. It has been noticed at the commercial fisheries on the River Bann (Northern Ireland) that silver eels held over until the following spring lose a little in weight.

The formulae expressing the length-weight relationship give a means of calculating the smoothed mean weight of an eel for its length. For yellow eels such computed weights have been obtained from the equation for the cubic regression line given on p. 117 and in Fig. 13. This equation, and not $3667 W/L^{3\cdot4709}$, has been used since the former takes in yellow eels of all lengths, whereas the latter considers only those of 45–70 cm. (Examples of weights worked out by both methods give results which are practically the same.) For the silver female eels the calculated weights were determined from the equation obtained from the regression line fitted to the fish of 45–70 cm. (Fig. 14) namely, $206\cdot6 W/L^{2\cdot7628}$; computed weights can therefore be found for fish within the length range.

Calculated weights have already been noted for the various age groups of yellow and silver eels (Tables 7 and 11).

In Table 15 the calculated weight for yellow eels of each centimetre length between 13 and 85 cm. is given. Comparison of the table with the length for weight data for German eels given by Walter (1910) and Ehrenbaum (1929) shows that for eels under 40 cm. long the relationship is much the same as that found for Windermere eels. In Table 16 the calculated weight for silver female eels of each centimetre length group between 45 and 70 cm. is given.

8.　GENERAL COMMENTS ON THE GROWTH OF EELS

In the preceding account some reference to the length and age and the length and weight relationships of eels in Continental waters has been made. In Table 17 the length for age of eels from some German, Italian, Dutch and French waters is given. It has been noted in the expression of these results that the time covered by the age index is not always the same (p. 31); in Table 17 differences due to this have been eliminated, age being recorded as in this report (p. 30).

In the Unterelbe and the Alster the eels grow at much the same rate as in Windermere until the IV group, a little more quickly from this to the VII group, and subsequently appreciably more

Table 15. *Yellow eels. Calculated mean weights for each cm. length group between 13 and 85 cm., observed means for 86–95 cm. (single observations) given in italics*

cm.	g.	cm.	g.	cm.	g.	cm.	g.	cm.	g.	cm.	g.	cm.	g.	cm.	g.	cm.	g.
—	—	20	11·7	30	41·5	40	103	50	216	60	404	70	697	80	1142	90	*1587*
—	—	21	13·6	31	*50·0	41	112	51	231	61	425	71	734	81	1160	91	—
—	—	22	15·7	32	51	42	121	52	246	62	453	72	773	82	1258	92	—
13	3·1	23	18·0	33	56	43	131	53	263	63	479	73	814	83	1315	93	—
14	3·9	24	20·6	34	61	44	141	54	280	64	506	74	854	84	1375	94	—
15	4·9	25	23·4	35	67	45	152	55	299	65	535	75	900	85	1444	95	*1785*
16	5·9	26	26·5	36	74	46	164	56	317	66	560	76	944	86	*1134*	—	—
17	7·1	27	29·8	37	80	47	176	57	337	67	595	77	990	87	*1587*	—	—
18	8·5	28	33·3	38	88	48	188	58	358	68	628	78	1043	88	—	—	—
19	10·0	29	37·2	39	95	49	202	59	380	69	662	79	1091	89	—	—	—

* Weight under 50 g. given to 0·1 g.

Table 16. *Silver eels, females. Calculated mean weights for each centimetre length group from 45 to 70 cm., observed means for 71–95 cm. (all are based on less than five specimens) in italics*

cm.	g.	cm.	g.	cm.	g.	cm.	g.	cm.	g.	cm.	g.
—	—	50	239	60	396	70	606	80	*1144*	90	*1872*
45	179	51	252	61	414	71	*692*	81	*928*	91	—
46	190	52	266	62	433	72	*690*	82	*1360*	92	*1814*
47	201	53	280	63	453	73	—	83	—	93	*1814*
48	213	54	296	64	473	74	*704*	84	*1360*	94	*1947*
49	226	55	311	65	493	75	—	85	*1348*	95	*2040*
—	—	56	327	66	515	76	*876*	86	*1388*	—	—
—	—	57	343	67	537	77	—	87	*1492*	—	—
—	—	58	362	68	559	78	*700*	88	—	—	—
—	—	59	378	69	582	79	*793*	89	*1623*	—	—

Table 17. *Length for age relationship of eels from various waters* (n.s. *indicates that the sexes are not separated*)

Place	Sex	I	II	III	IV	V	VI	VII	VIII	IX	X	No. eels examined
Windermere	n.s.	9·0	15·4	19·5	22·7	26·4	32·2	38·4	40·8	43·2	48·6	223
(a) Unterelbe, Germany	♂	11·8	14·5	19·3	24·8	30·9	35·5	37–39	—	—	—	603
	♀				26·0	33·8	39·3	40–47	60·0	60–66	—	
(b) Alster, Germany	♂	—	15·0	19·5	23·5	30·6	36·0	38–39	—	—	—	305
	♀				—	33·6	38·2	45·1	52·0	57·5	66·7	
(c) North German waters	♂	9·0	12·0	21·0	25·0	28·0	31·0	35·0	36·0	—	—	2 to 3 thousand
	♀				28·0	29·0	33·0	37·0	42·0	51·0	—	
(d) North German waters	n.s.	—	—	22·0	26·0	35·0	47·0	49·0	60·0	60·0	69·0	193
(e) R. Waal, Holland	♂	—	—	21·5	24·3	25·8	—	—	—	—	—	96
	♀				25·6	31·7	—	—	—	—	—	
(f) Comacchio, Italy (expt. ponds)	n.s.	11·9	23·0	32·4	55·0	—	—	—	—	—	—	—
(g) Comacchio, Italy (lagoons)	♂	10·9	15·5	21·0	26·0	31·5	36·5	35–39	—	—	—	53
	♀							41·0	46·0	52·0	59·0	
(h) Étang de Thau, France	♂	—	23·2	25·4	27·5	34·0	35·6	37·6	39·5	42·0	—	452
	♀					—	—	45·5	47·0	48·0	50·5	
(i) Canal Pont de Rousty, France	♂	—	—	28·2	34·1	36·6	40·4	45·0	36·0	—	—	125
	♀			31·4	36·7	42·4	51·0	—	—	—	—	

Sources of data: (*a*), (*b*) Ehrenbaum & Marukawa (1913); (*c*) Marcus, from Ehrenbaum (1929); (*d*) Wundsch (1916); (*e*) Tesch (1928); (*f*) Bellini (1910); (*g*) Haempel & Neresheimer (1914); (*h*) Hornyold (1928, 1931); (*i*) Hornyold (1930).

rapidly. The other results from German waters are those given by Marcus and Wundsch. The total number of eels examined by Marcus was large and the fish came from many waters; Wundsch examined only 193 individuals from eight different waters. The results obtained by Marcus and Wundsch have been summarized by Wulff to give the growth of eels in a north German water; this summary, as quoted by Ehrenbaum (1929), is given in Table 17. Of these results, those obtained by Marcus indicate that growth in the German waters is very little different from that in Windermere, but those obtained by Wundsch suggest that it is appreciably better. It is, however, somewhat misleading to compare the collective results from many waters with those obtained from Windermere, for when the data from the separate lakes and rivers investigated are considered (Marcus 1919; Wundsch 1916) it is found that growth differs greatly from place to place, for as Wundsch remarks, the minimum (Schmollen See) and maximum (Vilm See, Wundsch and Paprotker See, Marcus) values obtained for length and weight show a range of 30 cm. and ¾–1 lb. in 7–9-year-old eels.

The results given for Comacchio are those obtained from eels in experimental ponds (Bellini, 1907, 1910), and thus the figures quoted, although they refer to the fish which were reared under conditions similar to those of the lagoon, probably indicate a maximal and not a general rate of growth for the Italian waters. Growth is certainly very rapid and greatly exceeds that in any other European waters. The only other information about growth in the Comacchio lagoons is that provided by Haempel & Neresheimer (1914), who examined 53 eels from this place. These data, manifestly inadequate, show that growth in Comacchio is much the same as that in the Unterelbe and Alster. The growth of the few eels examined from the River Waal in Holland (Tesch, 1928) is much like those of German fish.

Of Hornyold's many studies of the growth of eels in France only those relating to two waters (both in southern France) are cited in Table 17. The pool of Thau appears to be near the sea, but it is not stated whether or not its waters are brackish. Growth there prior to V group is better than in any German water, but the length attained by the VIII, IX and X groups (71 specimens) is slower than in the Alster (27 specimens). The eels of the canal of Pont de Rousty, the waters of which are fresh, grow more rapidly than those in German waters, but not so rapidly as in the Italian lagoons. In both French waters growth is better than in Windermere.

This consideration of the growth of eels in different waters leads to the conclusion: (1) that, in general terms, Continental eels have a somewhat more rapid rate of growth than those of Windermere, in particular cases, as apparent from reference to the detailed data given by various workers, growth is considerably

more rapid, and (2) that there is, as between the different waters, a wide range in the rate of growth. From these two remarks it is reasonable to infer that the growth of the eel is appreciably affected by environmental conditions. The nature of these conditions and their effect upon growth is difficult to discuss, since precise information about the relationship existing between the eel and its environment is scanty, but the following brief remarks about the eel in relation to the factors of population density and food supply appear to be relevant to the matter.

Since it is known that the greatest quantities of elvers are found in the rivers of western Europe and that the supply diminishes progressively eastwards, it may be expected that the inland waters of the British Isles will receive more elvers* than the German waters and appreciably more than those of southern France and eastern Italy, and that in consequence they will have a greater population of eels per unit area. This difference in population density may be a significant factor in determining the rate of growth of the eels in the several waters. The fact that the eels of the River Severn grow more slowly than those of German waters, Marcus (1919) attributes to the enormous quantities of elvers entering the British river with the result that there is overpopulation and a consequent shortage of food. German workers frequently refer to the good growth made by elvers introduced into eel-free waters. Results obtained by Bellini (1907, 1910), from his experiments on the growth of eels, show that when the population of elvers is halved the fish grow more rapidly.

On some eel farms it is the practice to add food to the supply naturally present, from which it is evident that the food supply is regarded as a factor conditioning the growth of the eels. Scientific evidence as to the effect of food supply on growth is, however, practically confined to Bellini's investigations (1907). His experimental reservoirs included one which provided conditions comparable to those of the Comacchio lagoons and another with such conditions but having an augmented food supply. His results show that the length and weight attained for any age group was greater in the latter reservoir.

The foregoing comments, indicating that the growth of the eel is affected by environmental conditions, suggest that control of the growth of the fish is feasible, from which it follows that the eel pro-

* There is little information about the actual numbers of elvers entering these waters. It is well known that enormous quantities enter the River Severn, and local opinion maintains that there is a good run in the River Leven. Records kept for the small Lancashire river the Wyre, indicate that over a million elvers come into the river annually, and the detailed accounts kept by the Government of Northern Ireland of the captures of elvers at their trap on the River Bann (which virtually intercepts the whole run) show that 28–48 million enter the river annually.

ductivity of both natural and artificial waters may be subject to management. Any control, however, necessitates a knowledge of the biology of the eel in fresh water. At the present time little organized knowledge of this kind is available from British waters, and the value of the eel, actual and potential, as an economic fish in these waters, draws attention to the need for such biological studies.

9. SUMMARY

1. A study of the age and growth of the yellow eels and the age of silver eels in the Windermere catchment area, age determinations being based on otoliths and/or scales, has been made. The method of age determination is described and discussed.

2. Details of the age and length relationship and of the age and weight relationship for yellow and silver eels are given.

3. There is a small minority of female eels which become silver when older and larger than the majority. It is suggested that these older and larger fish have a more rapid rate of growth than the other eels, which growth, it is submitted, may have been present throughout the whole life in fresh water, but alternatively may have been assumed upon reaching a critical age and length.

4. Female silver eels may have spent from 9 to 19 years in fresh water, the mean being 12·27 years. These fish range from 47 cm. (18·5 in.) to 95 cm. (37·4 in.) in length and from 210 g. (7½ oz.) to 2040 g. (4½ lb.) in weight, with a mean length of 60·8 cm. (23·9 in.) and a computed mean weight of 410 g. (14½ oz.). The average weight of the female silver eels taken at the trap on Cunsey Beck is 396 g. (14 oz.).

5. Male silver eels form a very small proportion of the catch. They are very much smaller than the females, having a mean length of 39·9 cm. (15·7 in.) and average weight of 112 g. (4 oz.). They spend 7-12 years in fresh water, the average time being 9 years.

6. It is found that for the female eels the most common length at migration is 54-60 cm., but that although most fish of this length have spent 10, 11 or 12 years in fresh water some may have stayed a shorter or a longer time. It is therefore suggested that length and not age is the important factor inducing migration.

7. The length-weight relationship does not follow the cube law, and the change in shape and substance or both with length is found to be different in yellow and silver eels.

8. This difference in the length-weight relationship is shown to be, for female yellow and silver eels 45-70 cm. long, statistically significant.

9. The difference means that a silver female eel less than 58·06 cm. long is heavier than a female yellow of the same length, and that above this length a silver is lighter than a yellow of the same length.

10. This may be interpreted as indicating (1) that below 58·06 cm. the heavier and above 58·06 cm. the lighter yellow eels of each length become silver, or (2) that the transition from yellow to silver involves changes in the length and/or weight of the yellow eel. It is pointed out that the definitions of length-weight are not conclusive and that the relation of length-weight to silvering is at present not at all clear.

11. Length-weight coefficients show that the length-weight relationship ('condition') in yellow and silver eels shows no definite trend with age, that in yellow eels it is higher in the later part of the year, and that it is low in silver eels retained in tanks owing to loss of weight.

12. Consideration of the growth of eels in European waters leads to the conclusions that growth is more rapid in Continental waters than in Windermere and that growth may be affected by environmental factors.

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THE BIOTIC POTENTIAL OF THE SMALL STRAIN OF
CALANDRA ORYZAE AND *RHIZOPERTHA DOMINICA*

By L. C. BIRCH*, *Waite Agricultural Research Institute, University of Adelaide*

(With 2 Figures in the Text)

The rate of development of an infestation of insects in stored wheat is primarily determined by the potential geometric rate of increase or biotic potential of the insects. The value of the biotic potential under a given set of conditions will be realized if there is no restriction of food or accumulation of toxic products (Chapman, 1928). The biotic potential is in turn largely governed by the temperature and moisture content of the grain in which the insects develop. In this paper quantitative expression is given to the biotic potential of *Calandra oryzae* L. (small strain) and *Rhizopertha dominica* Fab. at different temperatures in wheat of different moisture contents.

The rate of increase in numbers in unit time (100 days) is given by the expression:

$$\text{Biotic potential} = \frac{E \times S}{2 \times D} \text{ (where sex ratio is unity)\dagger,}$$

where E = total number of eggs laid by one female, S = percentage survival of insects in their development from egg to adult, D = days taken to develop from egg to adult.

The formula is derived from the fact that the multiplication of one female in a single generation is given by (*a*) $\dfrac{E \times S}{2 \times 100}$ (sex-ratio unity). The multiplication in unit time will depend upon the rate of development from egg to adult. The rate of development is given by (*b*) $100/D$, which is the percentage development per day. The product of (*a*) and (*b*) gives the rate of multiplication. The biotic potential so defined is, of course, an average over a period of time, since it assumes a constant rate of egg-laying.

The values of the three factors necessary for the calculation of the biotic potential have been given in tables in previous papers (Birch, 1945 *a, b, c, d*). The biotic potential under different conditions as calculated from these tables was plotted in Fig. 1. Isopleths for the biotic potential were then interpolated; to avoid confusion only the isopleths are shown in the figure.

The relative positions of the lines for *R. dominica* and *C. oryzae* in Fig. 1 show that *R. dominica*

multiplies more rapidly at higher temperatures and in wheat of lower moisture content than *C. oryzae*. The maximum value of the biotic potential which was attained when temperature and moisture were most favourable, was of the same order for the two species (650). The points of intersection of isopleths of the two species having the same value show the combination of conditions under which the two species multiply at the same rate. This is only possible for *C. oryzae* and *R. dominica* at temperatures between 22 and 30° C. As the temperature is increased from 22 to 30° C. the moisture content of wheat at which the two species multiply at the same rate becomes higher.

The values of the biotic potential over the complete temperature range are shown in Fig. 2 for three different values of the moisture content of wheat (14, 11 and 10 %).* These curves are derived directly from Fig. 1. They show the range of temperatures, for a chosen value for the moisture content of wheat, at which one species multiplies more rapidly than the other. In wheat of 14 % moisture content (Fig. 2 *a*) *C. oryzae* multiplies more rapidly than *R. dominica* at all temperatures up to 31° C. At temperatures higher than 31° C. *R. dominica* multiplies more rapidly. In wheat of 11 % moisture content (Fig. 2 *b*) *C. oryzae* can only multiply more rapidly at temperatures lower than 23° C. In wheat of 10 % moisture content (Fig. 2 *c*) *R. dominica* multiplies at temperatures from 24 to 38° C. whereas *C. oryzae* cannot develop at all in wheat of this moisture content.

The trend of biotic potential with temperature is sigmoid up to the optimum temperature, after which the trend describes a reverse sigmoid curve. The sigmoid trend to the optimum temperature can be understood from the nature of the trend of the three factors which contribute to the value of the biotic potential. The values for the total number of eggs laid and the percentage survival are constant over most of the temperature range, increases in the value were recorded over about the first quarter of the

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* This work was carried out with the aid of a research grant from the Federal Grant to the University of Adelaide.

† It has been shown that the number of males and females arising from a random selection of eggs of *C. oryzae* and *R. dominica* is the same (Birch, 1945 *a*).

* The information in Fig. 2 describes in a quantitative way the difference in degree of multiplication of populations of *R. dominica* and *C. oryzae*. It disproves the statement made by A. J. Nicholson (1933, p. 140) that 'Chapman's hypothesis [of biotic potential] completely fails to help us to deal quantitatively with animal populations'.
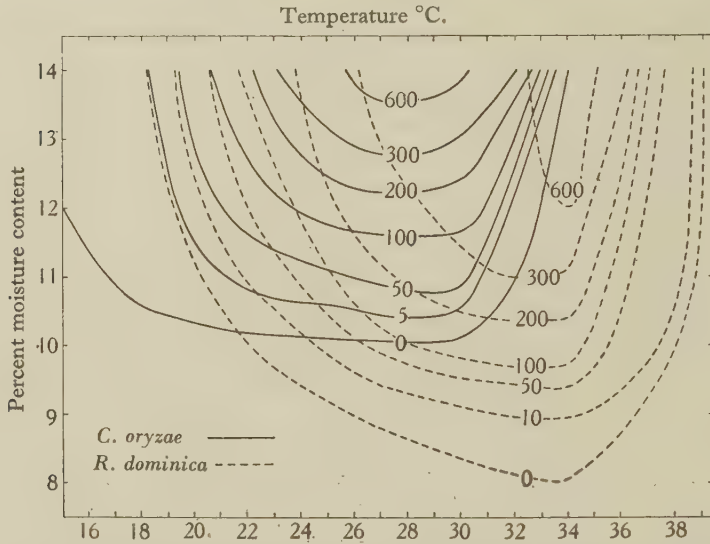
Temperature °C.

Fig. 1. Smoothed isopleths of the value $(S \times O)/(2 \times T)$, being the index of biotic potential or rate of multiplication in unit time (100 days) for *Calandra oryzae* (small strain) and *Rhizopertha dominica*. S=percentage survival in development from egg to adult; O=total number of eggs laid; T=days to develop from egg to adult.
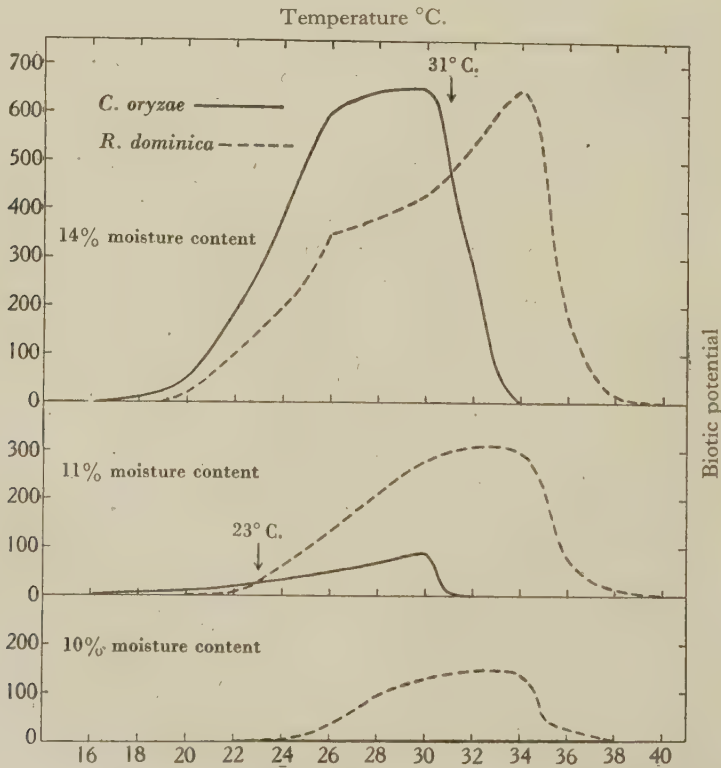
Temperature °C.

Fig. 2. Showing the relative speed of multiplication (biotic potential) of populations of *C. oryzae* and *R. dominica* over the complete temperature range for these insects in wheat of 14, 11 and 10 % moisture content. The graphs are derived from Fig. 1. The vertical arrow shows the temperature above which the biotic potential of *R. dominica* exceeds that of *C. oryzae*.

temperature range for egg laying (Birch 1945 c, d). The trend with temperature, to the optimum temperature of the values for the rate of development, was, however, sigmoid (Birch, 1945 a). The synthesis of these three trends must obviously be a sigmoid curve. The break in the sigmoid trend of the curve of *R. dominica* at 24° C. (Fig. 1 a) is a reflexion of the break in the temperature development curve at that temperature (Birch, 1945 a).

SUMMARY

The biotic potential of *Calandra oryzae* and *Rhizopertha dominica* has been calculated for various values of temperature and moisture content of wheat. These values cover the complete range of temperature and moisture at which the two species can multiply.

The index of the biotic potential used was:

$$\frac{\text{Potential number of eggs laid} \times \text{percentage survival in development from egg to adult}}{2 \times \text{days taken to develop from egg to adult}}$$

This gives the multiplication of one female in 100 days.

The maximum value for the two species was 650. In wheat of 14 % moisture content *C. oryzae* multiplies more rapidly than *R. dominica* at all temperatures up to 31° C. In wheat of 11 % moisture content the corresponding temperature is 23° C. In wheat of 10 % moisture content *C. oryzae* cannot multiply at all, but *R. dominica* multiplies at temperatures from 24 to 38° C.

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STUDIES IN THE DISTRIBUTION OF INSECTS BY AERIAL CURRENTS

THE INSECT POPULATION OF THE AIR FROM GROUND LEVEL TO 300 FEET*

By J. A. FREEMAN, *late University College of Hull*

(With 3 Figures in the Text)

E.M.N.

CONTENTS

1. INTRODUCTION

The work described in this paper, which has already been briefly summarized (Freeman, 1938), was carried out under the direction of Prof. A. C. Hardy as part of a more extensive investigation of the dispersal of insects by aerial currents. The first paper in this series has already appeared in this *Journal* (Hardy & Milne, 1938 b).

Collections of insects were made by flying series of nets from the 300 ft. masts of the Beam Wireless Station at Tetney, near Grimsby, in north Lincolnshire, at different heights and under different weather conditions and times of year. The collecting was begun by Mr P. S. Milne during May 1934 and

continued by myself during September and October and from March to November in 1935. The use of the wireless station was suggested by Prof. Hardy because of the height of the masts, their position in flat and varied agricultural country, their arrangement in a line covering five-sixths of a mile frontage, and also because they would enable nets to be flown in lighter winds than could be possible with kites and would also allow constant heights to be maintained.

The principal objects of the study were to estimate the quantity and composition of the aerial fauna from just above ground-level to nearly 300 ft.; to obtain a better understanding of the conditions governing insect drift; by using nets on the two end masts of the line and the one in the middle to obtain an idea of the varying density across the front at one time; and to discover what insects of economic importance were carried in this way and to relate the observations to the general problem of the wind dispersal of insects.

2. ACKNOWLEDGEMENTS

The work was made possible by the kind co-operation of Cables and Wireless Ltd. Many thanks are due to Mr Jupe, in charge of the station, and to his staff

for help freely given to me in carrying out the observations. I am also greatly indebted to Mr N. D. Riley, Keeper of Entomology at the British Museum (Natural History), for his interest in the work and to his staff for so kindly undertaking determinations of insects, as follows: Mr W. E. China (Hemiptera, except Aphididae); Mr F. Laing (Aphididae); the late Dr F. W. Edwards (Diptera); Dr K. G. Blair (Coleoptera); Mr G. E. J. Nixon (Hymenoptera). My thanks are also due to the following for kindly making determinations of various groups: Mr J. V. Pearman (Psocoptera); Dr G. D. Morison (Thysanoptera); Dr O. W. Richards (Diptera, Borboridae). I have also to express my appreciation of the opportunity afforded to me of a discussion with Mr P. A. Glick of the United States Department of Agriculture during his visit to England. I am also greatly indebted to Prof. A. C. Hardy for the direction of the work and for much help and criticism in the setting out of the results.

3. THE WIRELESS STATION, SURROUNDING COUNTRY AND METHODS OF COLLECTION

The Beam Wireless Station at Tetney lies about $5\frac{1}{2}$ miles south-east of Grimsby: the coast of the North Sea, bounded by a sea wall and a salt marsh runs in a north-west to south-east direction about 2 miles to the east. The area in which the station lies is thus bounded by the River Humber to the north and by the North Sea to the east. Around the station the land is very flat, having been to a great extent reclaimed from the sea. An extensive system of dykes drains the land, Tetney drain to the south of the masts being the largest. About 7 miles to the west the land is more hilly, where the Lincolnshire Wolds rise to a height of 300 ft.

The eight lattice masts are arranged in two series, a northern one of three masts and a southern one of five, the latter running almost due north and south. The masts used for the flying of nets were the northernmost (mast A) of the northern series of three and the northern (B) and the southern (C) of the southern series of five masts. The heights at which the nets were flown were 277 ft. (top), 177 ft. (middle) and 10 ft. (bottom or ground), above ground-level respectively. The masts stand in a permanent pasture, but the land around during the summer of 1935 carried a variety of crops: oats, barley, wheat, roots, potatoes, pulses, clover, together with market-garden crops and fruit trees in gardens in Tetney village to the south.

Each net was a cone of cheese-cloth 8 ft. long and 3 ft. in diameter at the mouth, which was held open by a wooden or wire hoop. Three cords leading to a swivel and clip served for the attachment of the net to the wire gantling on the mast. A small glass specimen tube was tied to a calico sleeve at the bottom of the net to receive the catch. A continuous wire cable, or gantling, was run through a block attached to the outer end of the cross-girder at the top of the mast. Each net was attached in turn by its clip swivel to a small cord loop tied to the wire cable.

A Marvin Kite Meteorograph, kindly lent by the Meteorological Office, was used to obtain a continuous record of the temperature, pressure, humidity and number of feet of air passing the instrument at a height of 216 ft. The instrument was slung from a spar fitted to the gantling of mast B, and an attached wind vane forced it to fly into the wind.

The nets were usually exposed for 3–6 hr. in all, generally from about 1030 G.M.T. to 1430 G.M.T. The time taken to haul each set of three nets was about 5 min. After being hauled down each net was placed in turn in a cyanide bottle for about 10–20 min. The small bottle, which generally contained most of the catch, was then removed and each net carefully examined for any insects caught on the fuzz of the net. Upon return to the laboratory the catches were sorted into families and later into species. Duplicates of unknown species were sent to various specialists at the British Museum and elsewhere for identification.

The actual number of insects taken in the nets cannot be simply compared from catch to catch, since the wind speed and the time of exposure of the nets were not constant. The wind velocity also increases with height, and Hellman (Napier Shaw, 1919) showed that for this type of country the formula $V = kh^{\frac{1}{5}}$ (V = wind velocity, h = height), is reliable for the calculation of wind velocity. Another factor to be considered was that the nets were found by experiment to filter about 80 % of the air passing them. It was decided to make catches comparable by calculating the numbers of insects in one million cu.ft. of air for each catch. This was defined as the 'density of insect population'. This amount of air may be regarded as that in a cylinder of air 27 miles long, of the cross-section of the mouth of the net or as the amount of air to a height of 23 ft. above 1 acre of ground. The average population density at each height on any day generally represents the mean of three net collections.

4. THE AERIAL FAUNA

(a) General

The predominant constituent of the aerial fauna was insects, but spiders and mites and a flora of the parts of plants were also present. The insects were mostly winged adults of small size, although a number of nymphs and true apterous forms were also taken. Generally the small size of the insects and the rare occurrence of large forms up in the air leads to the

conclusion that they are drifted involuntarily by the wind and have little or no power of determining the direction in which they are carried.

(b) Composition of the fauna

Diptera, Hemiptera and Hymenoptera were the dominant orders (Table 1). A few species (*Brevicoryne brassicae* L. (Aphididae), *Sciara* sp. (Sciaridae), *Pterodela pedicularia* L. (Psocidae), *Oscinis*

each. The aerial fauna is thus generally made up of large numbers of a few common species, although a great number of species actually occurs in the air from time to time. The various species showed marked differences in their vertical distribution.

(c) Variation in composition with height

The 'density of insect population' (total insects) decreased with height (Table 2): the number of

Table 1. *The total numbers of insects collected: (a) by orders and (b) by the commonest species*

No. of net collections (and occasions)	277 ft. 82 (30)	177 ft. 84 (29)	10 ft. 83 (31)	Total 249 (31)	% —
(a) Orders					
Thysanoptera	145	292	199	636	2·7
Psocoptera	138	269	1,984	2,391	10·2
Hemiptera	1,423	1,907	3,168	6,498	27·5
Coleoptera	183	345	794	1,322	5·6
Hymenoptera	448	757	2,710	3,915	16·6
Diptera (including Cecidomyidae and Borboridae)	611	1,215	7,078	8,904	37·2
Ephemeroptera, Lepidoptera and Collembola	7	8	8	23	0·2
Total numbers	2,955	4,793	15,941	23,689	100
Total families	59	63	75	79	—
Total named species	175	211	329	419	—
Total numbers (excluding Hymenoptera (except *Aphidius* sp.), Cecidomyidae and Borboridae)	2,669	4,306	14,301	21,276	—
Total named species (ditto)	158	186	279	342	—
(b) The commonest species					
1. *Brevicoryne brassicae* L. (Hemipt., Aphididae)	476	700	2,158	3,334	—
2. *Sciara* spp. (Dipt., Sciaridae)	103	314	2,069	2,486	—
3. *Pterodela pedicularia* L. (Psoc., Psocidae)	128	256	1,971	2,355	—
4. *Oscinis* spp. (Dipt., Chloropidae)	126	266	1,331	1,723	—
5. *Aphidius* sp. (Hymen., Aphidiidae)	162	270	1,070	1,502	—
6. *Leptocera* sp. (Dipt., Borboridae)	40	96	802	938	—
7. *Limothrips* spp. (Thysan., Thripidae)	98	220	89	407	—
8. *Swammerdamella brevicornis* Mg. (Dipt., Bibionidae)	4	21	275	300	—
9. *Spaniotoma aterrima* Mg. (Dipt., Chironomidae)	8	15	250	273	—
10. *Dilophus febrilis* L. (Dipt., Bibionidae)	14	27	182	223	—
11. *Myzus* sp. (Hemipt., Aphididae)	32	73	80	185	—
12. *Corticaria fuscula* Gy. (Col., Lathridiidae)	40	66	79	185	—
13. *Aphalara calthae* L. (Hemipt., Psyllidae)	86	87	11	184	—
14. *Anuraphis padi* L. (Hemipt., Aphididae)	43	34	100	177	—
15. *Scatella stagnalis* Fall. (Dipt., Ephydridae)	40	48	75	163	—
16. *Megaselia* sp. (Dipt., Phoridae)	17	36	107	160	—
17. *Kakothrips robustus* Uzel. (Thysan., Thripidae)	15	49	67	131	—
18. *Forcipomyia brevipennis* Macq. (Dipt., Ceratopogonidae)	1	7	114	122	—
19. *Phytomyza* spp. (Dipt., Agromyzidae)	20	24	71	115	—
20. *Enicmus transversus* Ol. (Col., Lathridiidae)	25	44	45	114	—
Nos. 1–5 (total), 5 species	995	1,806	8,599	11,400	49
Nos. 6–20, 15 species	483	847	2,347	3,677	14
Total (1–20)	1,478	2,653	10,946	15,077	63
Remainder (322 species)	1,191	1,653	3,355	6,199	27
Total	2,669	4,306	14,301	21,276	100

sp. (Chloropidae) and *Aphidius* sp. (Aphidiidae)), 5 in number, made up 49 % of the total numbers, a further 15 species formed 14 %, and the remainder, 322 species, were 27 %, leaving 10 % in the unidentified Hymenoptera. There were only 23 species having total numbers over 40 individuals and less than 100, and 60 species with numbers between 10 and 40. The remainder, 238 species, of which 112 occurred only once, had less than 10 individuals

species and of families represented at each height decreased at a lower rate (Table 3), mainly owing to the tendency for many of the common species, especially in the Diptera, to occur in much larger numbers at the 10 ft. level than at greater heights. Whilst the Diptera formed generally the greatest proportion of the fauna at ground-level, they were replaced by Hemiptera at heights above 100 ft. Together, these two orders formed a fairly constant

percentage, about 66 %, of the total numbers at each height. Coleoptera and Hymenoptera occupied fairly equal percentages at each height; high percentages were occupied by Thysanoptera at the upper levels and by Psocoptera at ground-level.

One-third of the species taken were confined to ground-level. Such species may be regarded as 'terrestrial' and those occurring above this level as 'aerial' forms. The former class formed a much higher proportion of the species of Diptera and

Table 2. *Constitution of the aerial fauna at different heights.*

	Mean population densities		
	277 ft.	177 ft.	10 ft.
Diptera	5·4	11·6	100·4
Hemiptera	12·3	17·7	51·2
Hymenoptera	3·6	6·7	39·2
Coleoptera	1·8	3·5	11·9
Thysanoptera	1·2	2·5	2·6
Psocoptera	1·4	2·6	34·9
Total insects	26·0	44·8	240·4

Table 3. *Mean population densities and average number of species at each height and the ratios of the values at the upper levels to those at ground-level*

		277 ft.	177 ft.	10 ft.	Total
1.	Average number of species	15	20	36	51
	Ratio	0·42	0·59	1	—
2.	Average number of families	15	18	26	30
	Ratio	0·58	0·69	1	—
3.	Average population density	26	45	240	—
	Ratio	0·11	0·18	1	—

Coleoptera than of Hemiptera, a further indication of the important position of the latter in the fauna of the upper levels (Table 4).

An examination of the frequency of occurrence of species (Table 5) shows that the number of species taken seven times or more (64), was relatively small. 'Aerial' species were generally taken more frequently than 'terrestrial' species and were also much more numerous. Diptera had the highest proportion in the higher frequencies and should be contrasted with Coleoptera, which, with about the

same number of species, were much less common. The large number of 'terrestrial' species taken six times or less is surprising, since, at ground-level, where the average population was highest, one would have expected to catch insects the most often. However, 'terrestrial' forms were mainly those occurring during the periods of maximum activity in June and September. The more common 'aerial' species were active often throughout the season and made up a basic aerial population, which was added to at the upper levels by the less common 'aerial' forms and at ground-level by the less common 'terrestrial' species.

A more detailed analysis, by families, of the composition of the aerial fauna at each height is shown in Table 6. The more numerous families, making up 92, 93 and 96·5 % of the total numbers at 277, 177 and 10 ft. respectively, fall into three main classes. The population densities of families making up group A decline much less rapidly than those of group C, so that the former made up 58 and 50 % respectively of the total populations at 277 and 177 ft. respectively, and only 25·5 % at the ground-level. The proportions of group C are the reverse. Group B contains certain families intermediate in character between A and C.

Whilst the population densities of certain families, e.g. Borboridae and Sciaridae, were high at the upper levels when contrasted with others at that height, they are not so high as would be expected from a consideration of their population densities at ground-level. On the other hand, the population densities of Aphididae, Thysanoptera and Psyllidae were often higher at the upper levels than near the ground. Many of the former families were only numerous at the upper levels at limited times of the year.

One may regard the families of groups A and B as being regularly dispersed by air currents, together with those families of group C whose numbers are large at the higher levels. The following list includes certain additional families, whose average population densities were too low to be included in Table 5: Groups A and B: Thripidae, Aphididae, Jassidae, Psyllidae, Curculionidae, Chrysomelidae, Lathridiidae, Chalcididae, Ephydridae, Agromyzidae, Tipulidae, Bibionidae, Opomyzidae, Drosophilidae; Group C: Psocidae, Aphidiidae, Sciaridae, Chloro-

Table 4. *The number of species at each height and of 'aerial' and 'terrestrial' species*

	277 ft.	177 ft.	10 ft.	All heights	Up to 277 ft.	Up to 177 ft.	Total Aerial	Total Terrestrial	Total All
Thysanoptera	4	4	5	4	0	0	4	1	5
Psocoptera	3	3	4	3	0	0	3	1	4
Hemiptera	42	46	53	27	15	17	59	14	73
Coleoptera	44	57	90	29	15	26	70	42	112
Diptera	62	72	124	44	18	26	88	52	140
Others	2	3	4	1	1	1	3	3	6
Total	157	185	280	108	49	70	227 (67 %)	113 (33 %)	340

Table 5. *The frequency of occurrence of species*

Frequency	1	2–6	7–11	12–16	17+	Total
Thysanoptera	1	2	1	0	1	5
Psocoptera	0	2	1	0	1	4
Hemiptera	26	31	12	4	0	73
Coleoptera	54	47	7	3	1	112
Diptera	47	60	14	9	10	140
Other groups	4	2	0	0	0	6
Total	132 (39%)	144 (41%)	35 (11%)	16 (5%)	13 (4%)	340 (100%)
'Aerial' species	63	101	34	16	13	227
'Terrestrial' species	69	43	1	0	0	113

Table 6. *The average population densities and the top/bottom and middle/bottom ratios of the most numerous families*

	Population densities			Ratios	
	277 ft. (top)	177 ft. (middle)	10 ft. (bottom)	T/B	M/B
A, high ratios					
Thripidae	1·2	2·5	2·6	0·46	0·96
Jassidae	0·9	1·19	2·5	0·36	0·50
Psyllidae	0·73	0·84	0·7	1·04	1·20
Aphididae	10·3	15·1	49·7	0·21	0·34
Lathridiidae	0·7	1·26	2·4	0·29	0·52
Chrysomelidae	0·4	0·58	1·1	0·36	0·53
Curculionidae	0·18	0·31	0·44	0·44	0·61
Ephydridae	0·45	0·57	1·6	0·28	0·36
Total	15·46	23·25	61·84	0·25	0·37
%	58	50	25·5	—	—
B, intermediate ratios					
Agromyzidae	0·31	0·60	2·3	0·13	0·26
Chalcididae	1·27	2·59	9·3	0·14	0·28
Total	1·58	3·19	11·6	0·14	0·27
%	6	7	5	—	—
C, low ratios					
Psocidae	1·4	2·6	34·9	0·04	0·07
Staphylinidae	0·4	0·97	5·6	0·07	0·17
Sciaridae	1·05	3·3	30·1	0·03	0·11
Chloropidae	1·38	2·48	21·9	0·06	0·11
Borboridae	0·46	1·27	12·7	0·04	0·10
Cecidomyidae	0·4	0·73	8·9	0·04	0·08
Chironomidae	0·18	0·45	6·2	0·03	0·07
Scatopsidae	0·06	0·20	3·9	0·01	0·05
Ceratopogonidae	0·07	0·13	2·9	0·02	0·04
Phoridae	0·18	0·61	2·7	0·07	0·23
Empididae	0·11	0·23	1·3	0·08	0·18
Proctotrupidae	0·36	0·72	7·0	0·05	0·10
Braconidae	0·35	0·52	4·5	0·08	0·12
Aphidiidae	1·16	2·31	15·9	0·07	0·15
Total	7·56	16·52	158·5	0·05	0·11
%	28	36	66	—	—
Remainder	2·00	2·74	8·86	—	—
%	8	7	3·5	—	—
Total (all insects)	26	45	240	0·11	0·19
%	(100)	(100)	(100)	—	—

pidae and certain genera only of Staphylinidae (*Tachyporus* spp., *Oxytelus* spp., *Atheta* spp.)

In contrast, certain groups are only likely to be dispersed short distances, since they show a very high proportion of the total catch in the nets of the lowest level; such families are Chironomidae, Ceratopogonidae, Mymaridae, Staphylinidae (in general) and most Heteroptera. A full comparative table compiled from all the available literature of the maximum heights reached by various families is given by Whitfield (1939).

It is possible further to list those species which occurred most frequently and in the greatest numbers in the top and middle nets and to contrast those with certain species which were taken frequently in large numbers in the lowest nets and either not at all or only in very small numbers in the upper nets. One may regard the former as typical 'aerial' species and the latter as 'terrestrial' species, and they may be listed as follows:

Aerial species: *Limothrips* spp., *Kakothrips robustus* Uzel, *Stenothrips graminum* Uzel, *Pterodela pedicularia* L., *Piesma maculata* Lap., *Deltocephalus pulicaris* Fall., *Cicadula sexnotata* Fall., *Aphalara calthae* L., *Macrosiphum granarium* Kby., *Myzus* sp., *Anuraphis roseus* Baker, *A. padi* L., *Brevicoryne brassicae* L., *Tachyporus hypnorum* F., *Corticaria fuscula* Gy., *Enicmus transversus* Ol., *Phyllotreta undulata* Kuts., *Chaetocnema concinna* Mm., *Sitona lineata* L., *Sciara* spp., *Dilophus febrilis* L., *Tachydromia* sp., *Megaselia* sp., *Phytomyza* sp., *P. flava* Fall., *Scatella stagnalis* Fall., *Hydrellia incana* Stenh., *Oscinis* spp., *Opomyza germinationis* L., *Aphidius* spp., *Leptocera sylvatica* Mg.

Terrestrial species: *Exaleochara morion* Grav., *Hypocyptus* sp., *Platystethus arenarius* Faure, *Spaniotoma aterrima* Mg., *Cricotopus sylvestris* F., *Forcipomyia brevipennis* Macq., *F. bipunctata*, *Dasyhelea flaviventris* Goet., *Swammerdamella brevicornis* Mg., *Drapetis* sp., *Thrypticus* sp., *Chloropisca glabra* Mg., *Leptocera crassimana* Hal., *Copromyza* sp., *Sphaerocera* sp., *Copromyza hirtipes* R.-D.

(d) Variation in the fauna during the year

The population density of total insects rose from March to June (Tables 7, 8), was low during July and part of August, rose towards the end of August reaching a maximum at the end of September, and then diminished to the end of October. The range of variation in population density and species is set out in Table 7.

There was a considerable variation in population density, numbers of species and of families, all of which tended generally to vary together (Tables 10–12), although during the autumn the numbers of species and families showed an earlier maximum (6 Sept. 1935) than the population density (27 Sept. 1935). Numbers of species and families and popu-

lation density varied together in the various orders. All had high values of population density during June, except Psocoptera, which were only numerous during September, whilst Thysanoptera were not taken in numbers after the end of August. Hemiptera showed well-defined June and late September peaks of numbers, due mainly to the large numbers of Aphididae (Table 13). The numbers of species, however, were more evenly distributed since Jassidae appeared during July and August in the greatest numbers, when this family tended to replace the Aphididae in the aerial fauna. Heteroptera (Table 12) showed well-marked June and September peaks of numbers of species. The high population densities and numbers of species of Coleoptera (Tables 12, 14) during May, June and September, were made up mainly by Staphylinidae, the most numerous family. Chrysomelidae were also numerous during June and, together with Lathridiidae, in August. The Diptera (Tables 12, 15) were very numerous in May owing to the appearance of large numbers of Borboridae and Sciaridae at all heights: of Chloropidae at the upper levels and of Chironomidae at ground-level. Except for the Chloropidae, these groups were not again numerous above ground-level. During June, many other families of Diptera were numerous, including Phoridae, Cecidomyidae, Agromyzidae and Ephydridae. Population densities of Diptera were low during August, but many groups appeared again in numbers at the beginning of September. This is to be contrasted with Coleoptera, whose autumn peak of abundance did not occur until the end of the month, whilst coinciding with Diptera in June. Hymenoptera (Table 16) had the greatest population densities in June, July and September. Aphidiidae appeared in very large numbers at the end of September, coinciding with a peak of Proctotrupidae, which, with Braconidae, were also numerous during June. Chalcididae tended to have large population densities during the summer, being especially numerous at the upper levels during August and at all levels in July and the beginning of September.

(e) Estimates of the numbers of insects in the air

The present observations enable a calculation to be made of the number of insects drifted per hour through a rectangle 300 ft. high and 1 mile broad, which is a little larger than the area actually bounded by the masts A and C. The average number per hour was 12,500,000, of which 75 % lay below 100 ft.: the maximum was 50,600,000 on 27 September 1934 and the minimum 457,900 on 23 August 1935. Even at the beginning of the year with 3,490,000 and at the end with 1,500,000 the numbers were relatively high. On days of maximum drift the wind was in the south-west and was carrying billions of insects out over the North Sea.

Table 7. *The average population density of total insects at each height on each of the days of sampling. The mean wind velocity for the period of exposure of the nets, and the air temperature and percentage relative humidity measured at 216 ft. and 1300 hr. G.M.T. for each of the days of sampling are also given*

Date	Population density 277 ft.	177 ft.	10 ft.	Wind velocity m.p.h.	Temp. °F.	% R.H.
1934: 30 May	10	21	—	21	56	60
9 July	16	35	147	9	70	42
10 July	18	43	233	12	76	40
11 July	46	77	268	12	83	37
12 July	18	63	190	10·5	73	52
13 July	15	25	211	10	64	60
25 Aug.	28	38	101	24	63	75
4 Sept.	50	93	367	12	67	65
11 Sept.	75	116	423	7·5	71	48
27 Sept.	63	111	836	18	52	62
31 Oct.	0	0·2	11	23	43	59
1935: 25 Mar.	1·4	2·2	40	25	56·5	62
10 May	1·4	7·2	45	23	50	68
17 May	31	86	356	12	52	48
7 June	2·4	11·6	66	35	64	75
14 June	35	57	387	24	68	63
21 June	69	121	711	14	75·5	71
28 June	31	49	381	14·5	72·5	64
5 July	—	—	59	35	69	72
2 Aug.	20	19	60	6	66	62
9 Aug.	7	5·4	31	12	65·5	65
16 Aug.	81	112	134	6	66	55
23 Aug.	2·7	8·2	17	6·5	62	73
30 Aug.	6·7	17·9	103	16	62	58
6 Sept.	29	33	190	22	61	52
13 Sept.	31	56	207	21	64·5	58
27 Sept.	69	135	1529	10	64	63
11 Oct.	14	15	82	22	52	59
18 Oct.	15	6	69	23	52	57
25 Oct.	3	5	30	8	46·5	54
1 Nov.	4	5	43	17	44·5	65

Table 8. *The variation in the average population density of total insects and the percentage composition of the aerial fauna (by orders), at each height from March to October, and the means for the whole period*

	Mar.	May	June	July	Aug.	Sept.	Oct.	Mean
277 ft. Other orders	—	—	1·6	0·4	1·2	—	—	0·9
Psocoptera	—	1·0	0·3	2·3	6·2	9·0	3·4	4·2
Thysanoptera	—	—	5·0	18·4	2·8	1·3	—	5·4
Coleoptera	—	5·6	6·8	0·7	12·1	8·2	3·1	7·1
Hymenoptera	—	—	12·3	18·9	12·8	16·0	6·1	13·8
Hemiptera	12·4	3·1	51·2	30·1	53·7	50·8	76·6	47·7
Diptera	88·6	90·3	22·8	29·2	11·2	14·7	10·8	20·9
Total (population density)	1·4	16·1	35·7	22·2	26·8	44·7	8·6	26·0
177 ft. Other orders	—	—	0·1	0·2	1·3	0·1	—	0·2
Psocoptera	8·3	—	0·6	0·9	10·1	7·5	4·2	5·8
Thysanoptera	—	—	4·2	21·9	4·6	0·1	—	5·7
Coleoptera	—	3·9	8·9	1·6	14·4	9·0	3·7	7·8
Hymenoptera	—	1·1	8·5	19·7	18·4	18·6	4·4	14·9
Hemiptera	—	2·6	48·0	24·6	40·0	49·0	71·7	39·5
Diptera	91·7	92·4	29·7	31·1	11·2	15·7	16·0	26·1
Total (population density)	2·1	46·1	61·8	48·8	34·7	75·1	8·8	44·8
10 ft. Other orders	—	—	—	0·1	1·6	—	—	0·1
Psocoptera	—	—	0·2	2·7	3·1	27·1	2·3	14·5
Thysanoptera	—	—	2·6	3·1	2·5	0·1	—	1·0
Coleoptera	1·5	8·5	7·9	1·6	7·7	3·6	10·5	4·9
Hymenoptera	0·5	1·3	13·1	18·6	24·5	18·4	12·2	16·3
Hemiptera	1·9	0·8	28·5	9·3	14·6	24·7	18·3	21·3
Diptera	96·1	89·4	47·7	64·6	46·0	26·1	56·7	41·9
Total (population density)	41·4	204·6	376·6	180·5	67·2	522·1	47·1	240·4

(f) Monthly distribution of species

A large number of species, 83 out of 342, were taken during both June and September, as contrasted with any other month or combination of months. Large numbers (39) were also common to May and September, June and October (29) as compared with the small number (6) taken in all

Table 9. *The maximum, minimum and mean population densities and number of species taken at each height*

Height (ft.)	Population densities			No. of species		
	Max.	Mean	Min.	Max.	Mean	Min.
277	81	26	0	47	15	0
177	135	45	1	49	20	2
10	1529	240	11	101	34	7
Total	—	—	—	127	45	8

months. There were also large numbers taken only during June (51) or September (34). This phenomenon is well marked in the various orders. A number of the species taken during June and September were not taken at any other time, and it would appear that the occurrence of large numbers of species at these times is associated with the lengths of the various life cycles. The times when they were taken in the nets would correspond to the periods when the adults were active in seeking food, breeding and, later, in finding winter quarters.

5. NOTES ON SPECIES OF SPECIAL BIOLOGICAL AND ECONOMIC INTEREST

(a) Thysanoptera

Limothrips cerealium Hal. and *L. denticornis* Hal. (the corn thrips) were taken in large numbers especially at the upper levels during June, July and August, corresponding to the times of migration from meadow grass to cereals in June, from cereal to cereal in July and back to meadow grass in August (Sharga, 1933). *Kakothrips robustus* Uzel. (the pea thrips) was common, especially at ground-level, during June.

(b) Psocoptera

Whereas *Pterodela pedicularia* L. occurred throughout the year in relatively small numbers, it appeared in swarms at the end of September in both years. The occurrence of *Lepinotus patruelis* Pearm. from March to September is of great interest, as it is a wingless form.

(c) Hemiptera

The capture of *Piesma maculata* Lap. (Piesmidae), the most numerous Heteropteron, is of interest, since *P. quadrata* Fieb., an allied species, is known to carry the virus of sugar-beet 'leaf curl' in Germany (Smith, 1931). One specimen of the very rare macropterous female of *Globiceps dispar* Boh. (Capsidae) was taken at 300 ft., and Mr W. E. China, in a letter to the

Table 10. *Total insects (by orders). The average population density at each height month by month and the mean for the whole period*

		Mar.	May	June	July	Aug.	Sept.	Oct.	Mean
277 ft.	Others	—	—	0·1	—	0·7	·	—	0·3
	Thysanoptera	—	—	1·8	4·1	0·8	0·6	—	1·2
	Psocoptera	—	0·2	0·1	0·5	1·7	4·1	0·3	1·4
	Coleoptera	—	0·9	2·5	0·2	3·2	3·6	0·3	1·8
	Hymenoptera	—	—	4·3	4·3	3·4	7·1	0·5	3·6
	Diptera	1·2	14·5	8·3	6·5	3·0	6·6	0·9	5·4
	Hemiptera	0·2	0·5	18·6	6·7	14·0	22·7	6·6	12·3
	Total	1·4	16·1	35·7	22·2	26·8	44·7	8·6	26·0
177 ft.	Others	—	—	—	0·5	0·3	0·1	0·1	0·2
	Thysanoptera	—	—	2·6	10·6	1·6	0·4	—	2·5
	Psocoptera	0·2	—	0·3	0·5	3·5	5·3	0·4	2·6
	Coleoptera	—	1·8	5·5	0·8	5·0	6·9	0·3	3·5
	Hymenoptera	—	0·5	5·3	9·5	6·4	14·0	0·4	6·7
	Diptera	1·9	42·6	18·4	15·0	3·9	11·8	1·4	11·6
	Hemiptera	—	1·2	29·7	11·9	14·0	36·6	6·2	17·7
	Total	2·1	46·1	61·8	48·8	34·7	75·1	8·8	44·8
10 ft.	Others	—	—	0·2	0·1	1·0	—	—	0·2
	Thysanoptera	—	—	9·9	4·6	1·7	0·4	—	2·6
	Coleoptera	0·6	17·8	30·0	3·9	5·2	18·0	5·0	11·9
	Psocoptera	—	—	0·6	4·9	2·1	142·8	1·1	34·9
	Hymenoptera	0·2	2·9	49·5	33·5	16·5	94·1	5·8	39·2
	Hemiptera	2·2	3·9	106·6	19·5	10·7	129·8	8·2	51·6
	Diptera	38·4	180·0	180·0	114·0	30·0	137·0	27·0	100·0
	Total	41·4	204·6	376·8	180·5	67·2	522·1	47·1	240·4

Table 11. *Total insects (by certain orders). Average number of species at each height per catch in each of the months of sampling and the mean for the whole period*

		Mar.	May	June	July	Aug.	Sept.	Oct.	Mean
277 ft.	Others	1	2	3	3	2	2	1	2
	Coleoptera	0	3	7	Neg.*	2	5	1	3
	Diptera	2	6	12	9	3	7	2	6
	Hemiptera	1	2	4	2	4	6	3	4
	Total	4	13	26	14	11	20	7	15
177 ft.	Others	0	2	3	4·5	2·5	4	0·5	2·5
	Coleoptera	0	5	10	2	3	8	2	5
	Diptera	5	12	14	12	3	9	3	8
	Hemiptera	0	2	6	3·5	4·5	7	2·5	4·5
	Total	5	21	33	22	13	28	8	20
10 ft.	Others	3	5·5	13	4·5	2	7	3	5
	Coleoptera	2	8	23	3	1	11	5	8
	Diptera	8	23	30	21	9	19	10	18
	Hemiptera	1	1·5	7	5	5	7	2	5
	Total	14	38	73	33·5	17	44	20	36

* Neg. = negligible.

Table 12. *Total insects (by orders): Hemiptera (certain families), Coleoptera (certain families), Diptera (certain families). Average number of species per catch (all heights) in each of the months of sampling and the mean for the whole period*

		Mar.	May	June	July	Aug.	Sept.	Oct.	Mean
A.	Other groups	3	7	16	5	0	4	2	5
	Thysanoptera	0	Neg.	3	2	1	Neg.	0	1
	Hemiptera	2	2	11	8	11	14	4	9
	Coleoptera	2	8	25	4	5	18	7	11
	Diptera	9	23	33	22	11	25	12	20
	Total named	16	40	87	41	28	61	25	46
B.	Heteroptera	0	0	3	1	0·5	2	0	1
	Jassidae	1	2	3	5	4·5	5	Neg.	3
	Aphididae	0	0·5	6·5	1	4	7	4	4·5
C.	Staphylinidae	1	6·5	12	2	0·5	10	4	6
	Chrysomelidae	0	Neg.	2·5	0·5	1·5	3	0	1·5
D.	Chironomidae	2	4	3·5	2	1	1	2	2
	Chloropidae	0	3	4	2	1·5	2·5	0·5	2
	Agromyzidae	0	1·5	5	3	2	2	Neg.	2

Table 13. *Hemiptera. The average population density at each height month by month and the mean for the whole period*

		Mar.	May	June	July	Aug.	Sept.	Oct.	Mean
277 ft.	Other families	—	0·1	0·3	—	—	0·4	—	0·2
	Heteroptera	—	—	0·1	0·2	0·1	0·3	—	0·2
	Psyllidae	—	—	—	0·1	0·6	2·6	0·1	0·7
	Jassidae	—	0·1	0·9	0·8	2·8	0·6	0·3	0·9
	Aphididae	0·2	0·3	17·3	5·6	10·5	18·8	4·8	10·3
	Total	0·2	0·5	18·6	6·7	14·0	22·7	5·6	12·3
177 ft.	Other families	—	0·3	0·5	—	Neg.	0·4	0·3	0·3
	Heteroptera	—	—	0·5	—	1·1	0·7	0·3	0·3
	Psyllidae	—	—	—	0·4	0·9	3·0	—	0·8
	Jassidae	—	0·1	1·0	1·6	1·8	0·9	0·1	1·2
	Aphididae	—	0·8	27·9	9·9	10·2	31·6	5·5	15·1
	Total	0	1·2	29·7	11·9	14·0	36·6	6·2	17·7
10 ft.	Other families	—	—	Neg.	1·5	0·3	Neg.	Neg.	0·2
	Heteroptera	—	0·1	2·4	0·5	0·5	Neg.	—	0·7
	Psyllidae	—	—	1·2	1·8	—	1·2	0·3	0·9
	Jassidae	0·8	0·6	3·0	3·0	4·3	3·0	0·3	2·5
	Aphididae	1·4	3·2	100·0	12·7	5·6	125·6	7·6	47·3
	Total	2·2	3·9	106·6	19·5	10·7	129·8	8·2	51·6

writer, remarks that this capture substantiates the idea that these forms take to flight and are scattered far and wide to form new colonies.

Almost all the species of Jassidae taken, of which those of the genera *Deltocephalus* and *Athysanus* were the most common, were mainly grass forms. The most numerous wingless species was *Cicadula sexnotata* Fall., which is a vector of various plant diseases. *Psylla mali* Schmidb. (the apple sucker) was represented by a small number of individuals taken in June, July and September. The greater number of Psyllidae at the upper levels is mainly due to the occurrence of *Aphalara calthae* L. in swarms during September.

Of Aphididae, the most numerous single family in the aerial fauna, the more common species of economic importance were *Macrosiphum granarium* Kby. (the grain aphid), *Anuraphis roseus* (Baker)

177 ft., although the Staphylinidae were by far the most numerous at the 10 ft. level. *Corticaria fuscula* Gyll. and *Enicmus transversus* Ol. (Lathridiidae) were the two most numerous species of beetles. With the exception of *Helophorus minutus* F. (Hydrophilidae), which attacks roots, and *Atomaria linearis* Steph. (Cryptophagidae) (the pigmy mangold beetle), all the species of economic importance taken were of the families Chrysomelidae and Curculionidae. The flea beetles, *Phyllotreta undulata* Kuts. and *Chaetocnema concinna* Mm., made up 132 of the total of 178 Chrysomelidae taken, and were present in numbers at all heights. The sudden appearance of these beetles on young roots in spring, especially on sunny days, is to be correlated with their lack of activity at temperatures below 60° F., and their carriage by wind currents. The most common weevils were *Sitona hispidula* F., *S. lineata* L. (the

Table 14. *Coleoptera (by families). Average population density at each height month by month and the mean for the whole period*

		Mar.	May	June	July	Aug.	Sept.	Oct.	Mean
277 ft.	Other families	—	0·3	0·5	0·1	0·5	0·7	—	0·3
	Staphylinidae	—	0·6	0·8	0·1	0·1	0·9	0·3	0·4
	Chrysomelidae	—	—	0·5	—	0·8	0·9	Neg.	0·4
	Lathridiidae	—	—	0·7	Neg.	1·8	1·1	Neg.	0·7
	Total	0	0·9	2·5	0·2	3·2	3·6	0·3	1·8
177 ft.	Other families	—	0·4	1·2	0·2	0·8	1·4	—	0·7
	Chrysomelidae	—	—	0·8	0·1	0·8	1·5	—	0·6
	Staphylinidae	—	1·4	2·2	0·4	0·1	2·0	0·2	0·9
	Lathridiidae	—	—	1·3	0·1	3·3	2·0	0·1	1·3
	Total	—	1·8	5·5	0·8	5·0	6·9	0·3	3·5
10 ft.	Other families	—	2·9	7·0	0·8	—	5·3	1·6	2·8
	Chrysomelidae	—	—	4·8	0·4	0·4	1·4	—	1·1
	Lathridiidae	—	—	3·6	0·2	4·3	3·4	0·1	2·4
	Staphylinidae	0·6	14·9	14·6	2·5	0·6	7·9	3·3	5·6
	Total	0·6	17·8	30·0	3·9	5·2	18·0	5·0	11·9

(the rosy apple aphis), *A. padi* L. (the leaf-curling plum aphis), and *Brevicoryne brassicae* L. (the cabbage aphis). All were taken commonly up to 300 ft., together with a number of other species which were not so numerous. The occurrence of Aphididae in the largest numbers during June and September is correlated with the times of migration of winged forms to and from the summer and winter hosts respectively. Thomas & Vevai (1940) should be consulted for the synonymy of certain of the Aphididae mentioned.

(d) Coleoptera

It is seen that 85% of the Coleoptera collected were distributed amongst four families, which were the most numerous at all heights. Staphylinidae were the most numerous family of Coleoptera both in numbers and species. The most common were of the genera *Tachyporus*, *Oxytelus* and *Atheta*, which were taken at all heights. The very even distribution of Lathridiidae should be noted, the numbers of this family being the greatest of any beetles at 277 and

pea and bean weevil) and *Apion flavipes* Payk. (the clover-seed weevil). Many of the Curculionidae were confined to June.

(e) Diptera

Of the 8901 individuals and 140 species, only 611 (62 species) were taken at the top level: 52 species were confined to the 10 ft. level. The four most numerous families (Sciaridae, Chloropidae, Borboridae and Cecidomyidae) occupied a high percentage of the total numbers (69%), but this decreased with height, mainly owing to the higher proportions occupied by families such as Agromyzidae and Ephydridae at the upper levels. Many families of Diptera, e.g. Scatopsidae and Ceratopogonidae, were much more numerous at ground-level than higher, and in general the Diptera may be considered as ground-loving.

Amongst the species of economic importance *Oscinis frit* L. was the most numerous, and its occurrence in numbers in May, July and September agrees fairly well with the observed facts of its life

history. It has also been recorded in the air in France and the United States, and Riggert (1931) found that the flies were most numerous at a height of 33–60 ft. and that they returned to the ground at night. Other Chloropidae, injurious to cereals, taken in the air were *Chlorops taeniopus* Meig. (the gout fly of barley), *Elachyptera cornuta* Fall. (which follows

at all heights, often in the same catches as many insects recorded as their prey. Richards (1930), in discussing the Borboridae (for which he uses the name Sphaeroceridae), states that they are 'all eminently terrestrial'. The relatively small numbers taken at the upper levels compared with those at the ground confirm this statement.

Table 15. *Diptera. The average population density at each height month by month and the mean for the whole period*

	Mar.	May	June	July	Aug.	Sept.	Oct.	Mean
277 ft. Other families	0·2	0·4	2·9	2·1	0·4	2·0	0·3	1·3
Agromyzidae	—	—	1·0	0·5	0·1	0·1	0·1	0·4
Cecidomyidae	—	0·9	0·6	0·8	0·3	0·1	0·2	0·4
Ephydridae	—	1·0	1·0	0·2	0·4	0·7	—	0·4
Borboridae	—	3·6	0·2	0·3	0·4	0·5	0·2	0·5
Sciaridae	1·1	4·0	1·6	1·1	0·2	1·1	0·1	1·0
Chloropidae	—	4·6	1·0	1·5	1·2	2·1	—	1·4
Total	1·3	14·5	8·3	6·5	3·0	6·6	0·9	5·4
177 ft. Other families	—	1·9	2·4	3·4	0·4	1·4	0·3	1·5
Bibionidae	—	1·2	1·5	Neg.	—	—	—	0·4
Chironomidae	0·2	1·1	0·3	0·7	0·3	0·2	0·2	0·4
Ephydridae	—	0·6	1·9	0·3	0·6	0·6	—	0·6
Agromyzidae	—	1·2	2·2	0·5	0·2	0·1	0·1	0·6
Phoridae	—	0·4	0·8	0·4	0·1	1·6	0·4	0·6
Cecidomyidae	0·2	1·5	·1·2	2·3	0·6	0·1	—	0·6
Borboridae	0·2	9·5	0·5	1·5	0·4	0·9	0·2	1·3
Chloropidae	—	9·7	2·4	2·7	0·9	3·3	0·1	2·5
Sciaridae	1·3	15·5	5·2	3·2	0·4	3·6	0·1	3·3
Total	1·9	42·6	18·4	15·0	3·9	11·8	1·4	11·8
10 ft. Other families	0·6	1·3	10·1	5·4	0·3	12·4	4·0	3·2
Empididae	—	1·9	2·7	1·9	0·9	1·1	0·1	1·3
Ephydridae	—	1·6	4·3	1·0	0·2	1·5	—	1·6
Bibionidae	—	1·7	8·7	0·2	0·3	3·2	—	2·3
Agromyzidae	—	2·0	6·1	2·6	1·9	1·9	0·2	2·3
Phoridae	—	1·7	4·0	2·5	1·0	6·1	0·4	2·7
Ceratopogonidae	—	1·5	2·1	4·5	4·6	3·4	0·5	2·9
Scatopsidae	—	3·6	9·8	8·8	—	2·4	—	3·9
Chironomidae	3·3	12·0	6·6	8·7	3·2	3·4	7·9	6·2
Cecidomyidae	3·8	11·6	22·9	15·0	2·2	5·4	5·7	8·9
Borboridae	8·9	36·4	18·2	11·4	1·0	18·8	4·3	12·7
Chloropidae	—	17·0	13·5	17·9	9·8	50·8	0·2	21·9
Sciaridae	21·8	87·8	71·0	34·1	4·6	26·6	3·7	30·1
Total	38·4	180·1	180·0	114·0	30·0	137·0	27·0	100·0

frit attack) and *Chloropisca glabra* Mg. (the last especially numerous at ground-level). *Hydrellia incana* Stick (Ephydridae), which attacks barley, was fairly numerous at all heights. Species injurious to grassland included *Tipula vernalis* Mg., *T. paludosa* Mg. and *Dilophus febrilis* L. (Bibionidae), the last being much more numerous near the ground than at the upper levels. Other species included *Psila rosae* Fall. (Psilidae) (the carrot fly), *Scaptomyza graminum* Fall. (Drosophilidae) and *Phytomyza flava* Fall., which attacks cabbages.

Of some biological interest was the occurrence of predaceous forms, Empididae and Dolichopodidae,

(f) Hymenoptera

Owing to the difficulty of specific identification in this order only a few specific determinations were made. The Aphidiidae occurred in very large numbers on days in September only, on the same occasions when large swarms of Aphididae were taken in the nets. Whilst most of the Hymenoptera tended to occur during the warmer months, Cynipidae persisted throughout the period of sampling. Of some interest was the capture, not only of one winged adult Dryinid but also an *Athysanus lineolatus* Brullé (Hemiptera, Jassidae), which was bearing a parasitic

Dryinid. Winged Formicidae were taken in August up to 277 ft. The wheat-stem sawfly (*Cephus pygmaeus* L.) was taken from time to time.

(g)   The occurrence of wingless forms

Thirteen Collembola, of which eight were taken on one day, were collected at all heights, being most

Table 16. *Hymenoptera.   The average population density at each height month by month and the mean for the whole period*

		Mar.	May	June	July	Aug.	Sept.	Oct.	Mean
277 ft.	Other families	—	—	0·9	—	0·1	0·3	0·4	0·5
	Braconidae	—	—	0·9	0·1	0·7	0·4	—	0·3
	Proctotrupidae	—	—	0·6	1·1	0·2	0·6	—	0·4
	Aphidiidae	—	—	1·2	0·4	0·6	3·9	0·1	1·1
	Chalcididae	—	—	0·7	2·6	1·8	1·9	Neg.	1·3
	Total	0	0	4·3	4·2	3·4	7·1	0·5	3·6
177 ft.	Other families	—	—	0·6	0·4	0·3	0·2	—	0·6
	Braconidae	—	0·4	0·9	0·6	0·6	0·7	—	0·5
	Proctotrupidae	—	—	1·3	2·8	0·8	1·2	—	0·7
	Aphidiidae	—	—	1·2	0·4	0·6	8·4	0·1	2·3
	Chalcididae	—	0·1	1·3	5·3	4·1	3·5	0·3	2·6
	Total	0	0·5	5·3	9·5	6·4	14·0	0·4	6·7
10 ft.	Other families	0·2	0·1	5·2	4·1	0·7	4·2	1·0	2·5
	Braconidae	—	0·8	8·9	3·4	5·6	6·5	0·6	4·5
	Proctotrupidae	—	0·4	18·5	8·6	2·2	8·8	0·2	7·0
	Chalcididae	—	1·1	10·4	16·1	6·9	15·0	0·2	9·3
	Aphidiidae	—	0·5	6·5	1·3	1·1	59·6	3·8	15·9
	Total	0·2	2·9	49·5	33·5	16·5	94·1	5·8	39·2

Table 17. *The number of individuals and species (in brackets) of the families of Thysanoptera taken at each height*

	277 ft.	177 ft.	10 ft.	Total
Aeolothripidae	2 (1)	1	10 (1)	13 (1)
Thripidae	119 (3)	284 (3)	177 (4)	580 (4)
Undetermined	24	7	12	43
Total	145 (4)	292 (4)	199 (5)	636 (5)

Table 18. *The number of individuals and species (in brackets) of the families of Hemiptera taken at each height*

	277 ft.	177 ft.	10 ft.	Total
Heteroptera:				
Tingitidae	7 (1)	15 (1)	30 (1)	52 (1)
Anthocoridae	0	2 (1)	8 (3)	10 (4)
Capsidae	2 (2)	3 (3)	5 (4)	10 (8)
Lygaeidae	2 (1)	8 (3)	6 (3)	16 (3)
Reduviidae	1	1	0	2 (1)
Undetermined	2	1	2	5
Total Heteroptera	14 (5)	30 (9)	51 (11)	95 (17)
Homoptera:				
Jassidae	86 (15)	94 (16)	153 (18)	333 (21)
Delphacidae	1 (1)	3 (2)	7 (3)	11 (4)
Cercopidae	9 (2)	6 (1)	5 (2)	20 (2)
Psyllidae	90 (4)	97 (5)	42 (5)	229 (7)
Aphididae	1223 (15)	1677 (13)	2910 (14)	5810 (22)
Total Hemiptera	1423 (42)	1907 (46)	3168 (53)	6498 (73)

common during August. Ten individuals of the wingless Psocid, *Lepinotus patruelis* Pearm., were taken, two only occurring at the 10 ft. level. A number of wingless nymphs of *Deltocephalus* sp. (Jassidae) were taken commonly at all heights throughout the year. One wingless Proctotrupid

6. RELATION OF THE AERIAL INSECT FAUNA TO THE VEGETATION

The majority of insects depend directly upon growing plants for shelter, food and breeding places, and the constitution of any insect population will therefore

Table 19. *The numbers of individuals and species (in brackets) of the families of Coleoptera taken at each height*

	277 ft.	177 ft.	10 ft.	Total
Staphylinidae	50 (21)	104 (22)	394 (38)	548 (47)
Lathridiidae	65 (2)	110 (2)	125 (3)	300 (3)
Chrysomelidae	37 (7)	54 (7)	86 (10)	178 (10)
Curculionidae	17 (7)	33 (7)	36 (9)	86 (14)
Hydrophilidae	2 (1)	18 (6)	24 (6)	44 (7)
Cryptophagidae	3 (1)	4 (2)	38 (4)	45 (4)
Nitidulidae	1 (1)	4 (2)	13 (2)	18 (2)
Scarabaeidae	1 (1)	0	16 (4)	17 (4)
Carabidae	5 (2)	9 (5)	4 (4)	18 (8)
Trichopterygidae	0	2 (1)	9 (1)	11 (1)
Others (7)	2 (1)	5 (3)	20 (9)	27 (12)
Undetermined	0	2	28	30
Total (1–4)	169 (37)	301 (38)	642 (60)	1112 (74)
As % total	93 (82)%	87 (66)%	81 (67)%	84 (66)%
Total (5–11)	14 (7)	44 (19)	152 (30)	210 (36)
Grand Total	183 (44)	345 (57)	794 (90)	1322 (112)

Table 20. *The numbers of individuals and species (in brackets) of the families of Diptera taken at each height*

	277 ft.	177 ft.	10 ft.	Total
Sciaridae	116 (5)	318 (3)	2126 (7)	2560 (8)
Chloropidae	136 (5)	276 (8)	1381 (10)	1793 (12)
Borboridae	44 (9)	106 (13)	908 (25)	1058 (27)
Cecidomyidae	43	64	637	744
Chironomidae	24 (5)	52 (7)	402 (10)	478 (11)
Scatopsidae	8 (4)	24 (2)	303 (8)	335 (9)
Phoridae	28 (3)	63 (4)	249 (4)	340 (4)
Agromyzidae	42 (4)	71 (4)	168 (7)	281 (7)
Ephydridae	64 (5)	71 (3)	119 (2)	254 (5)
Bibionidae	16 (1)	29 (2)	182 (1)	227 (2)
Ceratopogonidae	7 (3)	16 (4)	164 (8)	187 (8)
Empididae	13 (1)	18 (1)	101 (5)	132 (5)
Others (19)	53 (17)	90 (21)	220 (37)	363 (42)
Undetermined	17	17	118	152
Total	611 (62)	1215 (72)	7078 (124)	8901 (140)
1–4	339 (19)	764 (24)	5052 (42)	6155 (47)
As % grand total	(56%)	(63%)	(72%)	(69%)
5–12	202 (26)	344 (27)	1688 (45)	2234 (49)
As % grand total	(26%)	(28%)	(24%)	(25%)

was taken on 30 August 1935 at a height of 1100 ft. by means of a net flown from a kite.

The occurrence of wingless forms, in addition to spiders and mites and the parts of plants, tends to show that the winged insects occurring in the air are drifted in the same manner and have little power to determine their direction of motion, their wings having mainly the effect of increasing their buoyancy.

depend to a great extent on the type of vegetation in the area under consideration.

Most of the insect species taken were inhabitants of grassland (Jassidae and many Diptera), of cereals (*Limothrips* spp. and *Oscinis* spp.) and the weeds associated with them. The immediate surroundings of the masts and the greater proportion of the cultivated fields were of this nature, and the capture

of such insects in all wind directions is thus not surprising. Mushroom-inhabiting insects (*Philonthus* sp. and *Megaselia* sp.), of which a number were taken, could be derived from the surrounding grassland, in which large numbers of mushrooms grew. In addition dung-inhabiting forms (Staphylinidae, *Aphodius* sp., *Forcipomyia brevipennis* Macq., many Borboridae and *Scatophaga stercoraria* L.) and those

Table 21. *The number of individuals of the families of Hymenoptera taken at each height*

	277 ft.	177 ft.	10 ft.	Total
Aphidiidae	162	270	1070	1502
Chalcididae	150	279	658	1087
Proctotrupidae	62	108	497	647
Braconidae	37	56	318	411
Cynipidae	14	28	98	140
Mymaridae	5	5	56	66
Ichneumonidae	9	6	23	38
Formicidae	7	2	4	13
Tenthredinidae	0	0	3	3
Cephidae	0	0	1	1
Dryinidae	1	0	0	1
Undetermined	1	3	2	6
Totals, 1–4	411	713	2523	3647
	(92 %)	(94 %)	(94 %)	(93 %)
Remainder	37	44	187	268
Grand total	448	757	2710	3915

Table 22. *The number of* Kakothrips robustus *Uzel. taken on 14 June 1935*

	Mast		
	A	B	C
277 ft.	0	5	1
177 ft.	7	11	2
10 ft.	35	9	8
Total	42	25	11

Wind:
Direction S.S.W.
Speed 24 m.p.h.

(The line of masts runs approximately north and south.)

of decaying vegetable matter (Staphylinidae and many Diptera) would also find suitable breeding places in the fields around the masts. Insects known to be aquatic at various stages of their life histories (*Trechus 4-striatus* Schr., *Cercyon pygmaeus* Ill., Chironomidae, Ceratopogonidae and certain Borboridae) were taken in the nets in all directions of wind, carried from the dykes with which the country is intersected. Of insects known to favour maritime conditions two were taken in easterly winds, *Meromyza pratorum* Mg., which inhabits *Ammophila arenaria*, and *Megempleurus porculus* Bed., which is

known to be common on sand dunes. It was, however, surprising that no specific salt-marsh insects were taken, although the sea coast was bounded by a marsh and east winds might have been expected to carry such forms to the nets.

Many of the insects taken are known to be associated (in their immature or adult stages) with one or more plants. The presence of these plants around the masts led one to regard them as possible sources of insects taken in the nets and to attempt to correlate the presence of insects with the positions of cultivated fields and wild plants from which they might have been drifted.

It was sometimes possible to refer concentrations of insects in specific nets to nearby fields from which the wind might have carried them and also to determine those to which the wind might drift them. Peas and beans were common crops around the station. The large proportion of the total numbers of pea thrips (*Kakothrips robustus* Uzel) on 14 June 1935 in net A3 might have been due to the influence of the pea field lying to the south-west of mast A. The masts B and C were situated farther from possible sources of this species.

The occurrence of the cabbage aphis (*Brevicoryne brassicae* L.) in large numbers in net C3 during September when the wind was in the south-west, but not when it was in the north, seem to indicate that the source of these large numbers was a market garden lying to the south-west of mast C. There was also a tendency for a large number of other species to occur at a maximum in net C3 on the same day, including such enemies of Aphididae as *Aphidius* sp., Coccinellidae, Chalcididae and Proctotrupidae.

7. EFFECT OF THE WIND DIRECTION ON THE COMPOSITION AND NUMBERS OF THE AERIAL INSECT FAUNA

The average density of population was lower for winds from the east than from the west (Table 23). This may be attributed to the fact that westerly winds travelled over a much greater range of country before their fauna was sampled by the nets. However, whilst the largest population densities and the greatest variety of species were taken on westerly winds, there is evidence to show that for the same time of year the direction of the wind did not materially affect the composition of the collections. Thus during the beginning of September 1935, collections made in south-east winds (nos. 25 and 27,

Table 23. *The average population densities of total insects in east winds and west winds respectively*

	277 ft.			177 ft.			10 ft.		
Net	A1	B1	C1	A2	B2	C2	A3	B3	C3
Direction: East (11 collections)	22	15	25	40	30	42	136	127	133
West (11 collections)	41	47	36	81	80	64	359	391	644

Table 24) and in north winds (no. 26, Table 24) showed no significant differences either in population densities or in kinds of species.

It will be seen that the total number of species in any pair of days was about equal, and that there were actually more species common to the days of unlike wind direction than to those of like. It is of especial interest to note that one-third of all the Diptera taken were common to all days. The population densities of '26' and '27' were also fairly equal.

Again, with the exception of a large number of species which occurred only once during the year and then in small numbers, no insect species occurring commonly was confined to any one wind direction. For example, on 16 August (wind east) 1935, 32 species were taken in the middle and upper nets and must have reached that height over a distance of

be somewhat higher for broad-front winds than for narrow-front winds. The average population density of total insects and for many of the common families was remarkably even at each height over the front, especially at the upper levels (Tables 25, 27). At ground-level the greater average of net C3 was mainly due to the very large numbers of insects taken on two occasions. These were mainly made up of *Pterodela pedicularia* Linn. (Psocoptera) of *Brevicoryne brassicae* Linn. (Aphididae) and of *Aphidius* sp. (Aphidiidae).

The population density tended to vary with time consistently over the whole front. Of the series of catches made in June 1935, that on 21 June shows the maximum in all nets (Table 26). During June and September 1935 many families were represented in the catches but were not taken at other times of

Table 24. *The distribution of a number of species taken on three days of different wind direction*

Collection no.	Date	Wind direction	Wind velocity
25	30 Aug. 1935	S.W.	16 m.p.h.
26	6 Sept. 1935	N.	22 m.p.h.
27	13 Sept. 1935	S.W.	21 m.p.h.

	Numbers taken on				Numbers common to			
	25 and 26	25 and 27	26 and 27	All	25 and 26	25 and 27	26 and 27	All
Collembola	1	1	1	1	0	1	0	0
Psocoptera	3	2	3	4	1	2	1	1
Thysanoptera	1	1	1	1	1	0	0	0
Hemiptera	29	31	28	36	8	6	10	6
Coleoptera	24	24	27	32	5	2	8	2
Diptera	42	40	44	48	21	18	21	16
Total	100	99	104	122	36	29	40	25

2 miles (the distance to the sea) if none had been carried in from over the sea. Twenty-seven species were taken in the top nets, and if they had all come from the edge of the land they must have risen through the air at the rate of 14 ft. per min., since the speed of the wind was 6 m.p.h.

8. THE DISTRIBUTION OF THE POPULATION OVER THE COLLECTING FRONT

Since the masts run almost due north and south, the front sampled was at its maximum width (4400 ft.) in east and west winds and at a minimum (220 ft.) in north and south winds. The corresponding areas were 1,218,800 and 59,940 sq.ft. respectively.

It might be expected that the fauna would tend to be more evenly distributed when the front was narrow than when it was broad, especially when the irregular distribution of the various cultivated fields is considered. This, however, was not found to be the case: whilst from time to time there were considerable differences between the nets on the same day, on the average the population density tended to

Table 25. *The average population density on days of 'broad-front' winds and 'narrow-front' winds and on all days on which nets were flown at all heights*

(1) Broad front (winds N.N.W.–W.S.W. or E.N.E.–E.S.E.) (8 observations)

	A	B	C
277 ft.	31	24	31
177 ft.	59	37	58
10 ft.	193	179	181

(2) Narrow front (winds N.N.W.–N.N.E. or S.S.W.–S.S.E.) (7 observations)

	A	B	C
277 ft.	30	33	30
177 ft.	52	51	47
10 ft.	230	288	323

(3) Days when nets were flown at all heights

	A	B	C
277 ft.	31	31	30
177 ft.	59	53	52
10 ft.	250	259	394

year. However, when such groups did occur they appeared generally over the whole front.

A general analysis of the distribution of the more common families indicates that whilst the average densities at each height were usually fairly even,

unevenness of distribution occurred on some days. Sometimes a number of families would show excessive numbers in the same net. During July 1934 large numbers were associated with an even distribution. During September 1935 large numbers

Table 26. *The population densities of total insects at each point of sampling on 14, 21 and 28 June 1935*

	277 ft.			177 ft.			10 ft.		
	A1	B1	C1	A2	B2	C2	A3	B3	C3
14 June	38	39	30	63	74	41	479	373	322
21 June	78	77	65	161	118	96	504	904	780
28 June	38	32	28	90	18	49	316	363	278

was more evenly distributed at the upper levels. Near the ground the vegetation tended to induce local variations in the numbers of insects, but such are of small account when the general changes in the population from time to time are considered. These changes, occurring simultaneously over the whole front, indicate that insects behave similarly over a wide area, especially as the insects collected in the upper nets must have been picked up by the wind at some distance to windward of the nets. The greater evenness at the upper levels also shows that the wind has a dispersive effect which tends to eliminate the large variations in density found over the front near the ground.

Table 27. *The average population density of various groups for the whole period over the whole front*

	277 ft.			177 ft.			10 ft.		
	A1	B1	C1	A2	B2	C2	A3	B3	C3
Psocoptera	1·2	2·2	1·8	3·2	3·3	4·5	53·0	31·0	72·0
Thysanoptera	4·4	2·0	1·1	6·5	4·8	3·5	8·8	3·1	3·2
Jassidae	0·9	0·7	2·0	1·0	1·8	0·9	3·2	3·2	3·1
Brevicoryne brassicae	7·6	8·8	8·7	16·5	14·9	12·7	26·9	41·2	192·0
Aphididae	13·7	14·8	12·5	20·3	21·2	20·7	35·6	36·4	127·8
Aphidiidae	1·8	1·6	2·0	3·4	4·4	3·0	12·4	15·3	46·6
Chalcididae	1·2	1·1	1·9	3·1	2·6	3·8	9·3	11·6	11·6
Staphylinidae	0·1	0·9	0·6	1·5	1·2	1·0	9·9	7·9	7·7
Sciaridae	1·0	1·0	1·0	3·5	1·9	2·5	37·0	37·0	40·0
Cecidomyidae	0·5	0·5	0·4	1·1	0·6	0·7	11·8	13·9	11·9
Borboridae	0·27	0·24	0·4	0·9	0·8	1·1	162·0	193·0	167·0
Chloropidae	0·8	0·9	0·7	1·6	1·6	1·6	18·5	28·0	13·2
Total insects	31·5	31·4	30·2	59·0	53·0	52·0	250·0	259·0	394·0

were associated with a rather uneven distribution, especially at the lower levels. Whereas the maximum of the common families occurred in various nets on 13 September, they all coincided in net C3 on 27 September, when the maximum population densities of Psocoptera, Aphididae, Aphidiidae, Chalcididae, Sciaridae, Cecidomyidae, Borboridae, Proctotrupidae, and Lathridiidae occurred in this net. Those of Aphididae, Aphidiidae, Cecidomyidae and Chironomidae also occurred in net C3 on 11 October.

This tendency, exemplified by the Thysanoptera, Chalcididae, Psocoptera, Aphididae, Aphidiidae and Borboridae, of appearing in large numbers in specific nets would lead one to the conclusion that such groups tend to travel in swarms. Such concentration may be due to the proximity of host plants and other breeding places as shown for the relationship between the large catches of *Brevicoryne brassicae* L. in net C3 and the nearby market garden. There was a fairly close relationship between the distribution of Aphididae and of Aphidiidae: this has been noted for *Toxoptera graminum* Rond. (Aphididae) and *Aphidius* sp., which were observed to disperse together by Webster & Phillips (1912). The observations show that the distribution over the front was fairly even at all heights, and that in general the population

9. EFFECTS OF BIOLOGICAL AND METEOROLOGICAL FACTORS UPON THE OCCURRENCE OF INSECTS IN THE AIR

(a) General

The conditions affecting the activity and the numbers and kinds of insects in the air may be regarded as twofold. First there are biological factors such as the life history, habits and size of the species. These determine at what time of year the adult insect appears and whether it is likely to be carried by wind currents. Secondly, there are meteorological factors, climate and weather. The climate of any area generally determines the kinds of insects to be expected and the season of the year and time at which adult insects are likely to be active. The immediate factors of temperature, humidity and precipitation and wind velocity influence directly the activity of insects.

(b) Biological factors

(1) Life history and habits

It has already been stated that there was a distinct tendency for a large number of species and for the maximum number of individuals to occur in the air

during the months of June and September. Certain groups, however, tended to occur in large numbers also during May, during September and others during March and November. These phenomena can be ascribed mainly to the life histories of the various species. Thus many insects emerged from hibernation (Cryptophagidae and Chrysomelidae) or reached an adult stage (many Diptera) during spring and early summer. At this time the insects were naturally active in seeking food and in mating. This means that they were on the wing and were thus likely to be drifted by the wind. The coincidence of the activity of a large number of species, especially during June, indicates a similarity of habit and a similar effect of natural factors upon the insects at this time.

Certain families (e.g. Borboridae, Sciaridae and Staphylinidae) were only numerous at the upper levels in mid-May, whilst they maintained fairly high values at the lower levels at other times of year. This would indicate an active habit during May, since change of season is hardly likely to affect the insect's physical characters, which determine buoyancy.

During July and August the numbers of species and population densities were generally lower, although certain groups (Jassidae, Thysanoptera) became more numerous during this time. The absence during these months of many species taken during May and June, September and October, would indicate that they are then in an immature non-dispersing stage. Towards the end of August the increase of population density and in the numbers of species showed that a new generation was present and was active in feeding, mating and seeking breeding places or winter quarters.

In this connexion it is of importance to note that many of the species taken in the course of these experiments were also taken by other workers in England, France and the U.S.A. The similarity of the aerial fauna in the different countries emphasizes the fact that the habits of the insects, in addition to purely physical factors, are of great importance in determining whether they will be carried into the air. The difference of locality is also significant since Glick (1939, U.S.A.) and Berland (1935, France) found that Diptera were the most numerous at all heights, whereas the Aphididae were found, both in this study and by Hardy & Milne (1938b) in their kite collections, to be the most numerous.

(2) *Size*

Most of the insects taken were small and weak-flying forms such as Aphididae, Thysanoptera and small Diptera and Hymenoptera. Most of them were less than 5 mm. long and few exceeded 10 mm. However, a small number of forms of relatively large size, e.g. *Philaenus lineatus* L. (Cercopidae) 8 mm., *Sitona lineata* L. (Curculionidae) 6 mm., and *Tachyporus hypnorum* F. (Staphylinidae) 5 mm., were fairly

common at all heights, whilst *Nabis ferus* L. (Reduviidae) 8 mm., and *Harpalus aeneus* F. (Carabidae) 10 mm., were taken occasionally in the upper nets in addition to such bulky forms as *Sphaeridium scarabeoides* F. (Hydrophilidae), *Coccinella 10-punctata* L. (Coccinellidae), and *Scatophaga stercoraria* L. (Cordyluridae). The larger Diptera were only taken in winds of 14 m.p.h. or over, although a *Staphylinus siculus* Steir. was collected at a speed of 10 m.p.h.

The small size of the wind-borne forms is to be expected on physical grounds. The volume and consequently the mass increases by the third power, whilst surface only increases by the square. Since buoyancy depends on the ratio of surface to volume, the larger the insect the lower the buoyancy, unless the surface is increased by hairs or by a larger wing area. Increase of size, however, also means that the insect is better able to maintain itself in the air under its own power.

Some of the differences in the aerial fauna at ground-level and at the upper levels may be explained on these grounds. Staphylinidae, which were the most numerous near the ground, have less wing area and relatively larger bodies than the Chrysomelidae and Lathridiidae, which are more common at the upper levels. The various Hemiptera are also more buoyant forms than the Diptera Nematocera with small wings and long abdomen. The differences between the various groups of Diptera Acalypterae, however, are not so well explained on purely physical grounds. Thysanoptera, too, with their fringed wings are well adapted to wind carriage. It would seem that more information on this aspect should be obtained from an experimental study of the buoyancy of insects.

Although most of the species taken in the air were small, the presence of larger forms at certain times indicates that the habits of the insects must play some part in determining whether they are likely to be carried by wind currents. Thus the strong-flying Lepidoptera were hardly represented in the collections. The small size of the main elements of the aerial population implies that once in the air they must be drifted involuntarily by the wind, in the same manner as other organic and inorganic material suspended in the air.

(c) *Meteorological factors*

All meteorological observations were taken from the records of a Marvin Kite meteorograph, at a height of 216 ft. Temperature is expressed in degrees F., humidity as percentage relative humidity, and wind velocity in miles per hour. It should be noted that the wind velocity at ground-level was generally about half that at 216 ft.

(1) *Temperature*

The density of population and the number of species of total insects increased with rise of tem-

perature over the range 43–83° F. For individual groups and families the relation was not so well marked, although in general of all the groups Hymenoptera and Thysanoptera showed this relation the most clearly.

Table 28. *The ranges of the factors temperature, humidity and wind velocity*

Range no.	1	2	3	4	5
Temperature, ° F.	43–52	52–64	64·5–71	73–83	—
No. of observations	7	8	8	5	
Mean temp., ° F.	47·5	61	69	77	
Humidity, % R.H.	37–53	54–59	60–64	65–73	—
No. of observations	8	7	7	6	
Mean R.H.	46	57	62	69	
Wind velocity, m.p.h.	6–9	10–12	14–21	22–25	35
No. of observations	6	8	7	8	2
Mean velocity	8	11	18	23	35

The occurrence of certain species in the nets appeared to be limited by temperature. Thus all species of Heteroptera, all except four species of Jassidae, all except one Chrysomelid, and all except one Curculionid were taken at temperatures above 61° F. *Lepinotus patruelis* Pearm., a wingless Psocid, was confined to the range 48–66° F., Collembola to 62–70° F. Carabidae to 64–70° F., and Trichoceridae to 43–47° F. Only one species of Dolichopodidae was taken below 64° F. However, it would seem that the appearance of many species in the air was more to be associated with the life history than

with the immediate effect of temperature. Regular daily catches of the aerial insect population would throw more light on this problem.

These observations are generally in agreement with those of other workers. Glick (1939) found the maximum numbers of insects at 200 ft. at the temperature range 75–79° F., and Hardy & Milne (1938 b) made the maximum collections between 250 and 500 ft. at temperatures of 70–80° F. Minott (1922) showed that gipsy-moth larvae dispersed most readily at about 70° F.: the optimum range for the dispersal of the apple maggot was 75–85° F. (Phipps & Dirks, 1932). The dispersal of *Limothrips cerealium* Hal. occurred on bright sunny days (Sharga, 1933): this species was only taken at Tetney in appreciable numbers when the temperature was in excess of 68° F. McClure (1938) made his maximum collections at temperatures of 70–80° F.

(2) *Percentage relative humidity* (Table 30)

Population density generally showed a steady fall with increase of relative humidity from 37 to 73 %.

Table 29. *Average density of population at various ranges of temperature*

Range (see Table 28) ...	277 ft.				177 ft.			
	1	2	3	4	1	2	3	4
Thysanoptera	0	0·2	2·1	3·9	0	0·4	2·0	11·1
Chalcididae	Neg.	1·2	1·8	2·6	0·2	1·9	3·9	5·1
Braconidae	Neg.	0·1	0·9	0·6	0·1	0·4	0·8	1·2
Proctotrupidae	0	0·3	0·4	1·6	0	0·5	1·0	3·0
Ephydridae	0·3	0·6	0·4	0·8	0·2	0·4	0·7	1·4
Total insects	10	25	35	36	18	46	52	71
Hemiptera	4	13	17·5	15	4	22	22	26
Hymenoptera	0·3	5	4	6·5	0·4	9	8	11

Table 30. *Average density of population at various ranges of percentage relative humidity*

Range (see Table 28) ...	277 ft.				177 ft.			
	1	2	3	4	1	2	3	4
Psocoptera	1·8	1·5	1·2	0·8	3·8	2·8	2·5	0·5
Chrysomelidae	0·7	0·6	0·3	0·1	1·1	0·5	0·4	0·3
Borboridae	1·1	0·4	0·1	0·1	3·7	0·5	0·2	0·2
Chalcididae	2·6	1·1	0·6	0·5	4·6	3·0	1·1	0·5
Total insects	36	21	26	16	70	26	44	29
Hemiptera	11	11	15	10	19	10	24	15
Hymenoptera	7·6	2·3	2·2	1·6	14·7	4·8	3·2	3·2

Hemiptera, however, formed the principal exception, being most numerous under conditions of fairly high relative humidity. The highest humidity range (65–73) was unfavourable for all groups.

These observations agree with those of Hardy & Milne (1938 b), who found a general fall in the numbers of insects at 250–500 ft. with increase from 45 to 85 % R.H., humidities above 75–79 % being particularly unfavourable.

(3) *Precipitation*

Rain fell only on one day during the period of

exposure of the nets. The catch on that day (during August) was both very small for the time of year and also in comparison with those in March and November. One may deduce that, since conditions were otherwise favourable, that precipitation tends to prevent insects taking to flight or washes them out of the air. Moore & Anderssen (1939) have observed that *Frankliniella schulzi* Trybom. hides during rain.

(4) *Wind velocity* (Table 31)

Population density generally showed a tendency to rise from 6 to 12 m.p.h. and then to fall steadily with increase of wind velocity up to 35 m.p.h. The total number of species (all heights) rose to about 21 m.p.h. and then dropped considerably with further increase of wind velocity. The population

population density and wind velocity are in agreement with those of other authors, nearly all of whom agree that low wind velocities are much more favourable to aerial insect activity than high. Glick (1939) found the maximum number of insects in the air at 200 ft. when the ground-wind velocity was 5–6 m.p.h. and the least when it was 15–16 m.p.h. Hundertmark (1938) observed that the larvae of the nun moth (*Lymantria monacha* L.) would only take to flight when the wind velocity was not more than 5–6 m.p.h. *Euxoa segetum* Schiff. was not found in flight in Russia by Gruvanov (1937) when the wind exceeded 6–7 m.p.h. Uvarov (1931) quotes observations to show that honey bees are inhibited from flight by winds of 15–20 m.p.h. and mosquitoes by those of 8 m.p.h.

Table 31. *Average density of population at various ranges of wind velocity (m.p.h.)*

	277 ft.					177 ft.				
Range (see Table 28) ...	1	2	3	4	5	1	2	3	4	5
Jassidae	2·8	0·9	0·6	0·1	Neg.	2·5	1·3	0·9	0·2	0
Lathridiidae	1·8	0·6	0·6	0·4	0	3·1	0·6	1·1	0·4	0
Hymenoptera	3·7	3·1	6·3	2·0	0	8·3	7·4	10·3	2·5	0
Coleoptera	4·8	1·3	1·5	0·6	0	7·5	3·4	3·3	1·1	0
Total insects	31·3	31·7	29·7	14·2	1·8	46	68	51	20	5·8
Hemiptera	14·9	13·5	14·9	8·0	0	17·2	26·5	20·8	10·1	0
Diptera	4·9	9·2	5·1	2·5	1·8	8·4	21·8	11·5	4·7	5·8

Table 32. *The ranges of the factors temperature, humidity and wind velocity in combination*

Temperature, ° F.	t	43–64	T	64·5–83
Humidity, % R.H.	h	37–59	H	60–73
Wind velocity, m.p.h.	w	6–12	W	14–35

Numbers of observations and mean values

	TH	Th	tH	th	TW	Tw	tW	tw	WH	Wh	wH	wh
No. of observations	6	7	7	8	5	8	10	5	8	7	8	5
		m.p.h.				% R.H.				° F.		
Mean value of 3rd factor	18	11	16	18	66	50	59	60	62	58	64	64

density of Hymenoptera rose to 21 m.p.h. and then fell, whilst the population of Coleoptera fell sharply from 6 to 10 m.p.h., and then declined slowly with increase of wind velocity. Diptera was the only group well represented at the maximum wind velocity.

The very small population densities recorded at 35 m.p.h. would appear to be explained by the tendency for insects to take cover from high winds. On one of the days when the wind velocity was 35 m.p.h. many insects, not taken in the nets, were seen flying in the shelter of ditches. Moore & Anderssen (1939) recorded that *Frankliniella schulzi* tended to hide during high winds, and Watkins & Miner (1943) found that *Psila rosae* L. tended to be more numerous in flight with reduction of wind velocity. The European corn-borer (*Pyrausta nubilalis* Hübn.) is stated to be inactive during high winds (Caffrey & Worthley, 1927).

The general observations on the relation between

(5) *The factors temperature, humidity and wind velocity considered in combination*

The results of the examination of each pair of factors is shown in Table 33 and Fig. 1 for temperature and humidity, in Table 34 and Fig. 2 for temperature and wind velocity, and in Table 35 and Fig. 3 for humidity and wind velocity. As shown in Table 32, the dividing lines (T–t, H–h, W–w) were drawn so that there was, as far as possible, the same number of observations on either side. The dividing lines lay at 64° F., 60 % R.H. and 13 m.p.h. respectively. In the discussion the high values of the factors are indicated by T, W and H and the low by t, w and h respectively. In the figures the values for the mean population densities in each quadrant are plotted on an axis at 45° to the main axis with the value for zero lying at the intersection of all axes in the centre.

From Table 33 and Fig. 1 (temperature and humidity) it is seen that for most groups population densities tended to increase in the directions *t* to *T* and *H* to *h*, with a marked indication that *Th*

The combined effect of temperature and wind velocity is shown in Table 34 and Fig. 2, and it is seen that in general there was increase of population density from *t* to *T* and from *W* to *w*, the latter

Table 33. *Average density of insect population under various conditions of temperature and relative humidity in combination*

| | 277 ft. | | | | 177 ft. | | | |
	tH	*TH*	*th*	*Th*	*tH*	*TH*	*th*	*Th*
Total insects	15	32	20	39	40	50	35	69
Diptera	2·3	5·7	5·6	7·2	6	12	13·5	13·5
Hemiptera	10	18	8	15	16	26	9	22
Hymenoptera	0·5	4·1	3·3	5·6	1·3	4·7	8·1	12·4
Coleoptera	1·2	2·0	0·7	4·2	2·3	4·2	1·3	7·1
Jassidae	0·4	1·2	0·2	2·2	0·4	1·5	0·4	2·3
Chalcididae	0·2	1	1	3	0·6	1·5	1·6	6·4
Braconidae	0	0·7	0·1	0·8	0·1	0·8	0·4	1·0
Aphididae	9	17	6	18	15	23	6	30
Cecidomyidae	0·1	0·5	0·3	0·8	0·3	1	0·4	1·4
Chloropidae	0·7	0·3	1·7	0·6	1·7	0·4	3·4	0·5
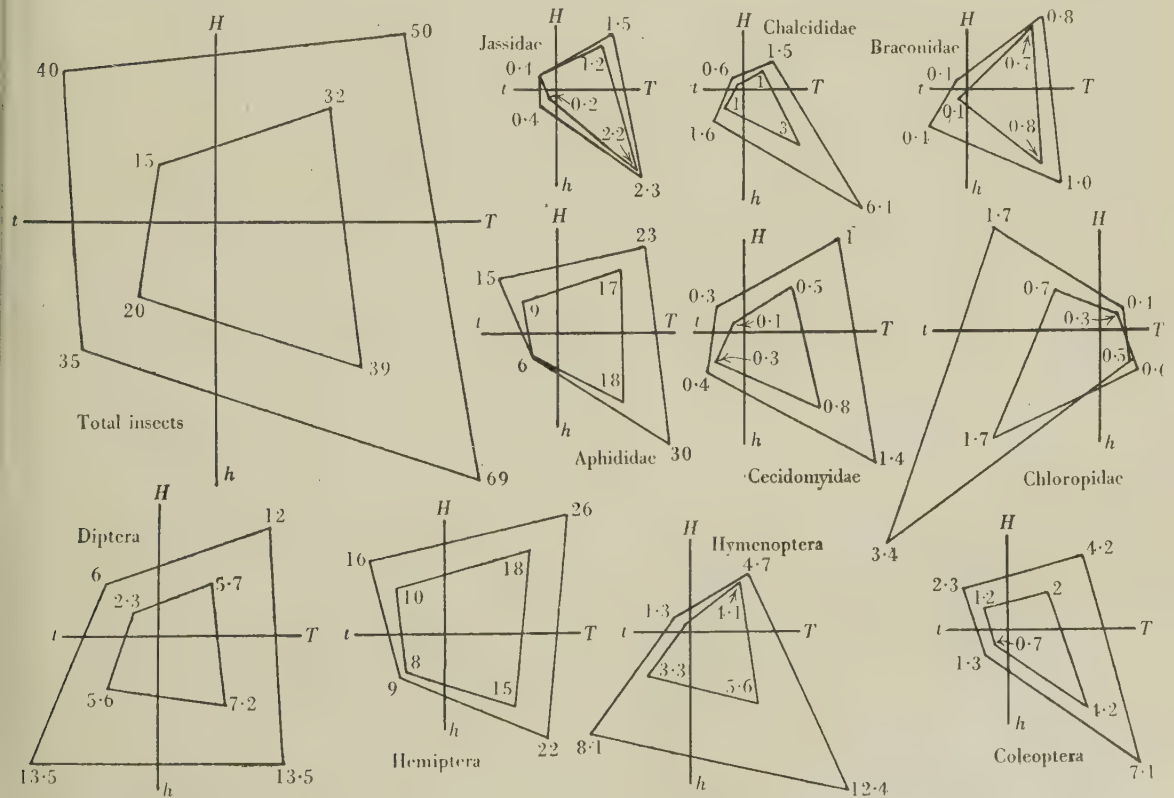
Fig. 1. Average density of insect population under various conditions of temperature and relative humidity in combination (Table 33).

provides the most favourable conditions. Exceptions to this general rule are the Hemiptera and Chloropidae; the former showed increase of population density from *h* to *H* and from *t* to *T*, whilst the latter showed increase from *T* to *t* and from *H* to *h*.

effect being more marked in the temperature ranges below 60° F. With certain exceptions *Tw* provided optimum conditions.

When wind velocity and humidity are considered in combination (Table 35 and Fig. 3), it was found

that in general there was increase of population density from H to h and from W to w, optimum conditions being generally, but not always, wh. For Hemiptera, particularly Aphididae, increase was shown from h to H and from W to w, giving optimum

It appears from this study that, for total insects, whilst all three factors exercise some influence on the number of insects in the air, temperature has the major influence, especially at the higher levels. Population density, in general, increased with rise

Table 34. *Average density of insect population under various conditions of temperature and*
wind velocity in combination

	277 ft.				177 ft.			
	tW	TW	tw	Tw	tW	TW	tw	Tw
Total insects	15	38	25	35	22	65	51	59
Diptera	3	7	7	6	5	15	19	12
Thysanoptera	0	1·7	3·4	0·1	0	3·5	0·6	5
Coleoptera	0·4	2·7	1·9	3·5	0·9	5·8	3·5	5·9
Jassidae	0·2	0·8	0·5	2·2	0·3	1·1	0·7	2·3
Lathridiidae	0·2	1·1	0·5	1·3	0·2	2·0	0·7	2·4
Chloropidae	0·8	0·4	2·1	1·4	1·9	0·7	6·1	2·3
Chrysomelidae	0·1	0·5	0·1	1·1	0·1	0·8	0·2	1·6
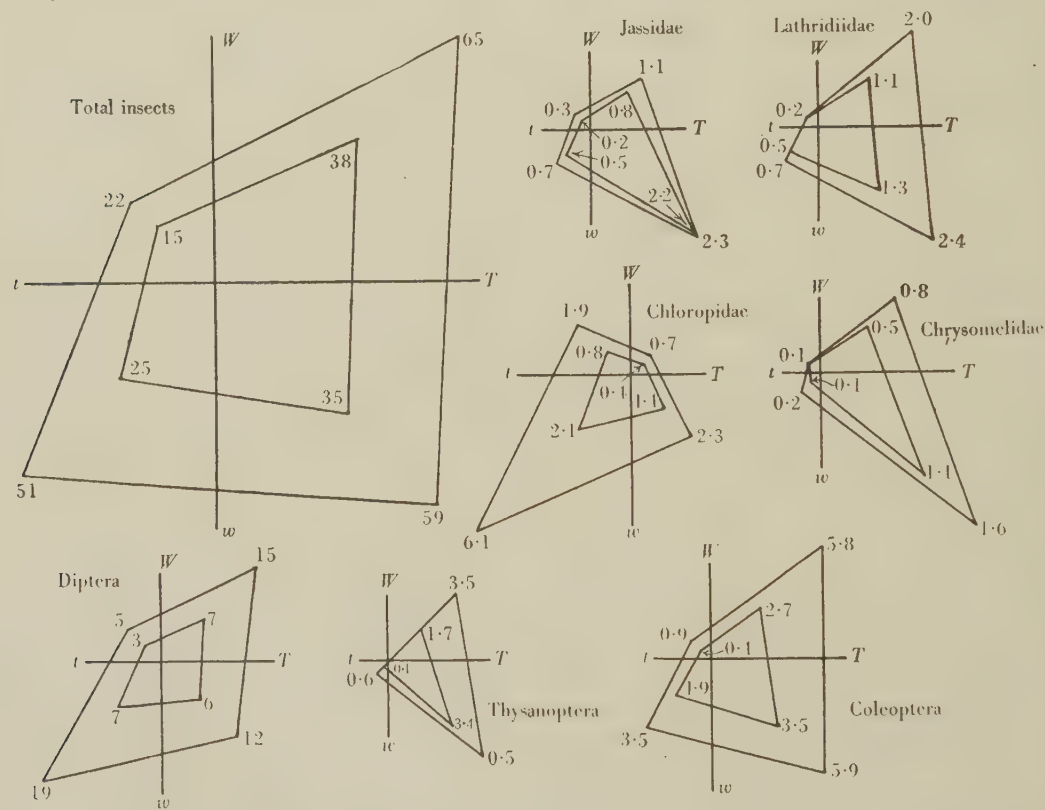
Fig. 2. Average density of insect population under various conditions of temperature and wind velocity in combination (Table 34).

conditions in wH, which, owing to the high proportion of this group in the fauna at the upper levels, helps to explain the somewhat even distribution of the figure for total insects. It will be noted, particularly, that the Hymenoptera have very low population densities in the H range.

of temperature under all other conditions. This is in general agreement with the conclusion reached by Glick (1939, 1942). The average population density at each height (total insects) under the most unfavourable combination of conditions (WtH) was 8 (277 ft.), 14 (177 ft.) and 59 (10 ft.), and under the

most favourable conditions (*wTh*) was 42 (277 ft.), 74 (177 ft.) and 266 (10 ft.). Whilst the maximum population densities at the upper levels in the air were recorded under *TH* those at ground-level were taken under *tH*, an effect largely to be explained by the differences in composition of the aerial fauna at

The observations for the Aphididae are in fair agreement with those of Davies (1938), who showed that the optimum conditions for the dispersal of *Myzus persicae* Sulz. in June in Scotland were: temperature in excess of 65° F., relative humidity below 75 %, and wind velocity below 5 m.p.h.

Table 35. *Average density of population under various conditions of wind velocity and relative humidity in combination*

	277 ft.				177 ft.			
	wW	*WH*	*wh*	*Wh*	*wH*	*WH*	*wh*	*Wh*
Total insects	23	21	35	22	38	37	67	32
Hymenoptera	1·2	2·5	4·7	5·7	2·3	3·1	10·5	9·6
Hemiptera	16	11	12	11	24	17	18	12
Aphididae	14	5	10	8	22	16	15	8
Chalcididae	0·8	0·4	2·4	1·3	1·1	0·8	5·3	2·1
Lathridiidae	0·6	0·4	1·3	0·5	0·7	0·7	1·4	0·8
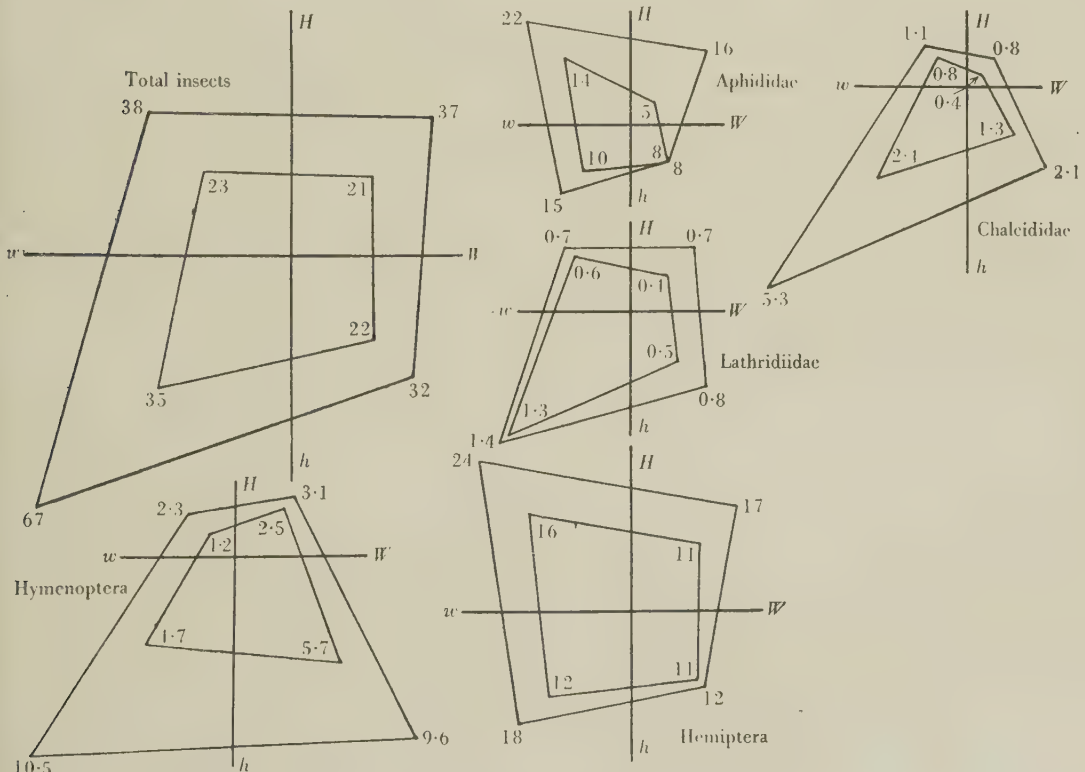
Fig. 3. Average density of population under various conditions of wind velocity and relative humidity in combination (Table 35).

the different levels, particularly the higher proportion of Hemiptera at greater heights. It has already been demonstrated that Aphididae develop the greatest numbers in the aerial fauna under conditions of high humidity. The conditions under which the population densities at each height were most nearly equal (for total insects) were *Twh*.

Thomas & Vevai (1940), as the result of five years' trapping in north Wales, found that the optimum conditions for aphid migration were: temperature over 75° F., relative humidity 80 %, and wind velocity less than 2 m.p.h. (ground-level). Greenslade (1941) showed that the corresponding conditions for the dispersal of the raspberry aphid

(*Capitophorus fragariae* Theob.) were: wind velocity less than 3 m.p.h., temperature over 60° F., and relative humidity below 70 %. The discrepancies between the various observations may be set down principally to variations from one species to another; the dominant species in the Tetney collection was *Brevicoryne brassicae* L.

10.　DISCUSSION

The evidence presented in this paper supplements the work of other authors (Coad, 1931; Collins & Baker, 1934; Berland, 1935; Hardy & Milne, 1938 *a* & *b*; Glick, 1939; and McClure, 1938), especially with information regarding the wind-borne population at levels up to 300 ft. It has been shown that there is, over both land and sea (Hardy & Milne, 1937; Hardy, 1938), a rich aerial fauna, consisting of weak-flying insects of small size and high buoyancy, whose presence has been demonstrated up to a height of 16,000 ft. These forms, being carried involuntarily by the wind, are dispersed by air movements as contrasted with the migration of moths, butterflies and locusts, which are sufficiently powerful to maintain their flight if necessary against the wind.

In the study of the vertical distribution of the fauna it has been shown, in this paper, that whereas the 'density of total insect population' decreased rapidly with height, especially up to about 150 ft., the proportion of Hemiptera (48 % at 300 ft.), especially Aphididae, increased and that of Diptera decreased (21 % at 300 ft.). Hardy & Milne (1938*b*) found that the percentage of Hemiptera was about 30–40 % of the total insect population in the air between 150 and 2000 ft. Aphididae were the most numerous family in the Tetney collections as well as in the kite collections of Hardy & Milne over the land (1938*b*) and the sea (1937). Other observers have recorded few Aphididae and found Diptera to be the most numerous group at all heights (Berland (1935), France; Coad (1931), Collins & Baker (1934), Glick (1939) and McClure (1938), all in the United States). In the present work it has been demonstrated that the aerial fauna is determined to a considerable extent by the nature of the local vegetation, and that the distribution of insects over the front, almost 1 mile broad, was remarkably even. As the physical properties do not vary, it would appear that differences in the composition of the aerial fauna are due to dissimilarities in the fauna at the lower levels, this being in turn determined by the general character of the flora at the various places of collection. However, there were quite a number of species, particularly in the 'aerial' group which were common to the collections made in England, France and the U.S.A. Such evidence indicates that these species are normally dispersed by wind currents.

The differences between the fauna at the ground and upper levels are so marked that one may consider that the aerial population can be split into 'terrestrial' and 'aerial' components, the latter being dominant at heights above 150 ft. This subject has been fully discussed in the body of this paper and lists given of the families and species forming typical elements of the 'terrestrial' and 'aerial' faunas. Whitfield (1939, p. 399) has considered the subject and points out that most of the insect species taken from aeroplanes are of the 'terrestrial' type and therefore more likely to have found their way into the aircraft when on the ground than in the air.

The largest numbers of insects occurred in the air during spring, early summer and autumn, corresponding to the times of greatest activity of adults in the search for food, breeding places and winter quarters (autumn). For example, very large numbers of Aphididae were taken in the air at the time of alternate flights from winter to summer hosts and back; most of the Staphylinidae were taken during May, June and September. Certain families (Jassidae, Lathridiidae) tended to occur fairly evenly throughout the warmer months. These observations correspond closely with those of McClure (1938), who has shown that definite peaks of activity occur in the aerial fauna near ground-level during mid-spring and early autumn and possibly also at mid-summer. Glick (1939) found that maximum activity occurred in May, followed by a slight decline during the summer months, with increase again during the autumn. It is not necessary for insects to be active throughout the year to achieve successful dispersal: they need only take advantage of seasonal winds. For example, the cotton-boll weevil (*Anthonomus grandis* Boh.) made its greatest advances in the southern states of the United States by means of winds during its period of autumn activity (Hunter & Pierce, 1912). The rapid spread of the Colorado potato beetle (*Leptinotarsa 10-lineata* Say) from the Rocky Mountains to the Atlantic coast in about 15 years was almost entirely due to carriage by winds during the short period in autumn when the beetles are active (Tower, 1906). Dispersal in Europe similarly appears to occur by dispersal during limited periods (Feytaud, 1939). The main dispersal of the pink bollworm (*Pectinophora gossypiella* Saund.) in south Texas was effected by the prevalent winds during September (McDonald & Loftin, 1935). It thus appears unnecessary for insects, which have achieved successful dispersal by wind, to be active for more than a limited part of the year. This may be considered in its application to the present work. The greatest variety and numbers were found at Tetney during June and September. Certain groups, e.g. Sciaridae and Borboridae, were only numerous above the 10 ft. level during May, whilst it was only during September that Psocidae

were taken in large numbers in the upper nets. If the winds at such times were to carry and finally deposit the insects in favourable surroundings, then the various species would achieve successful dispersal, especially if the insects occurred in large numbers at these times.

Insects may be carried up into the air by their own activity in flight (*Loxostege sticticalis* L. (Mel'nichenko, 1936); *Limonius californicus* Man (Shirck, 1939)), by eddy currents set up by normal horizontal air movement and by convection currents. The last were observed on one day at Tetney, when a period of calm, accompanied by hot sun, preceded the establishment of a definite easterly drift. During this period convection currents, induced by the heating effect of the sun upon the grass, were observed to be agitating the nets, and it is certain that these currents were carrying insects up into the air. Convection currents have been observed up to great heights, the effects being experienced by aircraft up to 10,000 ft. There are many records of convection and other low velocity up-currents of air carrying insects upwards. Guppy (1925) records the carriage of butterflies up to the crater of Mauna Loa in Hawaii by a trade-wind current. Whymper (1892) quotes Humboldt who had observed various insects at heights of 16,000–18,000 ft. in the Andes and ascribed their presence to currents carrying them up the mountain sides. Bruce & Thornley (Tutt, 1901) observed hundreds of aphids on the snow at the summit of Ben Nevis; they considered that the insects had been carried up by warm currents. Tomlin & Sopp (1901) made collections of Coleoptera on Snowdon and found the fauna at the upper levels to contain a well-marked lowland component. Many of the species taken were recorded as members of the aerial fauna at Tetney.

Once carried up into the air insects may meet strong winds which may carry them long distances. McDonald & Loftin (1935) found strong steady south-west winds at heights of 3000–4000 ft. in south-west Texas and took pink bollworm moths at that height. Felt (1924–9) considered that these upper air currents are of considerable importance in the dispersal of insects, and quotes as a typical example the carriage of the cotton moth (*Alabama argillacea* Hübn.) which breeds in the cotton fields of the southern United States and which appears in large numbers during autumn at lights in southern Canada and the north-east United States. He also considers (1928) that insects carried by upper air currents may drop when passing over lakes and snowfields and mountain tops owing to the production of downward currents. The sparse distribution of insects at great heights leads one to suppose that whilst some of these occurrences of insects in snowfields may be explained in this way there is considerable evidence which indicates that the insects may often be carried up the sides of mountains by rising currents and then dropped on the snow. In the same way insects may be deposited in lakes and in the sea after being drifted out at moderate heights by low-velocity wind currents. Successful dispersal by low-velocity winds has been demonstrated for *Loxostege sticticalis* L. which is carried at heights of 250–300 ft. (Mel'nichenko, 1936).

For ecologically successful dispersal it is necessary that the insects should arrive alive and with viable eggs. Wind dispersal may result in the insects being deposited in the sea or in a lake or river or on a snowfield, or the insect may be killed by exposure to low temperatures at great heights. Even if the insect is living when it reaches earth again it may be deposited in a place where climatic conditions are such that it cannot breed. All the insects collected at Tetney were living when taken; those taken by Hardy & Milne (1938b) up to 2500 ft. were all living, as were those taken by other workers, even up to a height of 16,000 ft. (Glick, 1939). The fungal spores taken by the Stratosphere Expedition at heights of over 36,000 ft. were all viable (W—, R.T.P. 1938). Experimental work on this problem was carried out by Noble (1936), who showed that adult females of the pink bollworm kept at a temperature of 60° F. (that recorded at 3000 ft.) from 1 to 7 days would lay fertile eggs. Examples have already been given of the dispersal by wind currents of insects to such unsuitable sites as the tops of mountains, snowfields and to places outside the climatic zones in which the species can breed. Thus the cotton moth (*Alabama argillacea* Hübn.) does not breed north of the cotton belt in the United States, and many insects drifted out over the Great Lakes are washed up later on the shore (Snow, 1902). Many thousands of Colorado beetles were washed up on the eastern shore of the New England coast after being drifted out to sea by winds (Tower, 1906). The spruce aphids (*Dilachnus piceae* Pz.) dropped in North-East Land (Elton, 1925) were unable to establish themselves owing to the absence of their food plant. It should not be forgotten, however, that many migratory species of Lepidoptera and locusts may travel to areas where the conditions make it impossible for them or their progeny to breed.

Records exist of the carriage of insects long distances by storms, but such dispersal is to be regarded as catastrophic. The extensions of the area of the cotton-boll weevil (*Anthonomus grandis* Boh.) was greatest after equinoctial storms, which carried the beetles north-east (Hunter & Pierce, 1912), whilst Fenton & Dunnam (1928) showed that the flight of the beetle was not affected by moderate winds. The 'blue page' moth was recorded as being blown from Trinidad to Barbadoes, 160 miles, by a hurricane (Hurd, 1920); and there are many records of butterflies and locusts being blown on to ships out of sight of land. Elton (1925) recorded large numbers of the spruce aphid (*Dilachnus piceae* Pz.) and the hover

fly (*Syrphus ribesii* L.) from the surface of the snow in North-East Land, Spitzbergen; these insects were probably carried there by strong south-east winds from the Kola Peninsula, the nearest place with spruce, 800 miles across the sea. It was shown in the present observations that high winds are not favourable for large numbers of insects in the air, and on one day of maximum wind velocity (35 m.p.h.) many insects were seen flying in the shelter of dykes and were not taken in the nets which were exposed to the full force of the wind.

In addition to the examples of catastrophic dispersal by storms, there is much evidence of the importance of prevailing winds. It is considered that the carriage of gipsy-moth larvae (*Porthetria dispar* Boh.) by the prevailing winds accounted for the dispersal of this species in New England (Collins, 1915; Schedl, 1936), the optimum wind velocity for this dispersal being 10–12 m.p.h. (Minott, 1922), although larvae were captured at wind velocities of 2–23 m.p.h. The dispersal of the spring-grain aphis of the U.S.A. (*Toxoptera graminum* Rond.) was explained by wind carriage in a north-easterly direction, the aphids having been observed to fly with the wind (Webster & Phillips, 1912). Females of the Hessian fly (*Mayetiola destructor* Say) were proved to have been carried over 3 miles by the wind, and the general distribution of this species in Kansas was in the direction of the prevailing south-south-west winds (McColloch, 1917). The European corn-borer (*Pyrausta nubilalis* Hübn.) was dispersed with the aid of winds and in an experiment marked species were recovered which must have been drifted by wind across Cape Cod Bay, a distance of 20 miles (Caffrey & Worthley, 1927). Quayle (1916) showed that young scale insects (*Saissetia oleae* Bern.) were drifted 400 ft. by the wind, and that their dispersal over an orchard was directly related to the direction of the prevalent winds at the time of activity of the young forms. Felt & Bromley (1937) consider that the spread of *Scolytus multistriatus* Marsh. in New England is due to drift in the direction of prevalent winds. *Eutettix tenellus* Baker (Jassidae; Dorst & Davis, 1937) and *Paratrioza cockerelli* Sulz. (Psyllidae; List, 1939) were shown to have been drifted long distances by wind from desert areas in south Arizona to south Colorado and Utah at the rate of some 200 miles in 2 days. Gaines & Ewing (1938) showed that the dispersal of *Psallus serialis* (the cotton-flea hopper) could be explained by carriage in the direction of the prevalent winds. Clark (1938) considers that the Coccid *Eriococcus coriaceus* Mark. was drifted by wind from the South to the North Island of New Zealand, which it reached in 1921, the original introduction having been in 1900. Barber (1939) found the Ortalid *Euxesta stigmatias* Loew. in sweet-corn fields in extreme south-east Florida in March and considered that it could have been drifted by

the wind from the West Indies. Many other examples are given by Whitfield (1939).

The Tetney observations bring out the importance of wind drift and moderate winds, rather than storms, since, while storms may occasionally disperse insects for great distances, wind movement every day tends to carry insects steadily over the country. It is to be observed, however, that the prevalent winds at Tetney during the periods of maximum activity of the insects (June and September) were south-west. The aerial population was thus being carried out over the North Sea. The observations of Hardy & Milne (1937) show that the wind is capable of carrying insects to a distance of 150 miles from land, and it is likely that the insects would be carried across the North Sea to the Continent. Furthermore, it was shown in the Tetney observations that the maximum numbers of insects were found in the air under conditions of high temperature and low humidity, which are more usually associated with winds of moderate and low velocity than with high winds and storms, which are often characterized by low temperature and precipitation, at least in temperate countries. These latter conditions were shown to be those under which insects tend to take shelter. One may conclude that the maximum effective dispersal is achieved by winds of low velocity, which steadily carry large numbers of insects over the country.

Many of the discoveries of the influence of wind in the dispersal of insects were made in the United States in the course of work on the control of noxious insects such as the gipsy moth (*Porthetria dispar*), the Colorado beetle (*Leptinotarsa* 10-*lineata*), the Hessian fly (*Mayetiola destructor*) and the cotton moth (*Alabama argillacea*). In the Tetney Collections 44 species of insect pests were recorded, of which 17 species or allied species were also collected by Felt & Chamberlain (1935) in the United States, 4 by Berland (1935) in France and 10 by Hardy & Milne (1938 b) in England, whilst many other (non-pest) species were common to the various aerial collections. Amongst the more important agricultural pests taken at Tetney were: *Oscinis frit* L. (frit fly of oats), recorded in the air in England by Hardy & Milne (1938 b), in France by Berland (1935), in Germany by Riggert (1931) and in the United States by Collins & Baker (1934); *Cicadula sexnotata* Fall., also recorded in England by Hardy & Milne (1938 b), in the United States by Felt & Chamberlain (1935); the corn thrips (*Limothrips cerealium* Hal.), also recorded in England by Hardy & Milne (1938 b), and in France by Berland (1935); flea beetles of the genera *Phyllotreta* and *Chaetocnema* in France by Berland (1935), in the United States by Felt & Chamberlain (1935) and by Glick (1939). Certain Aphididae were common to the English and American collections.

Evidence has been put forward to show that a

number of common pests were taken in the air in the course of collections in various countries. It has also been shown that many pests, particularly in the United States, have been effectively dispersed by prevailing winds. This factor should therefore be taken into account in the preparation of control measures. In this connexion one may speculate on the ultimate fate of the large numbers of insects drifted out over the North Sea, particularly during June and September. A number fall into the sea and are sometimes taken in the course of plankton-net collections (private communications to the author from marine workers), whilst others remain in the air (Hardy & Milne, 1937). The evidence leads one to conclude that there must be a constant interchange of the smaller wind-borne species between this country and the continent of Europe, especially when the 150 miles distance from land at which the North Sea collections were made is contrasted with the mere 20 miles across the English Channel. Felt & Chamberlain (1935) reviewed the subject of ground quarantines in the light of the results of aerial faunal collections and state that such quarantines, maintained at enormous cost, have been useless in preventing the spread of insects which can so easily be drifted into new territory by wind currents. It follows that no legal quarantine should be applied for the attempted prevention of the introduction of any insect pest into the United Kingdom until its status as a wind-dispersed form has been investigated.

II. SUMMARY

1. The insect aerial population above an area of agricultural land in Lincolnshire was sampled at heights of 10, 177 and 277 ft., over a front of 4400 ft., by nets flown from the masts of a beam wireless station.

2. The population consists mainly of small weak-flying insects of high buoyancy drifted involuntarily by the wind. Diptera were most numerous near the ground, Hemiptera were dominant above 100 ft., and Aphididae was the most numerous family at all heights. Over half the total number of insects collected were of the species *Brevicoryne brassicae*, *Sciara* spp., *Pterodela pedicularia*, *Oscinis* spp., *Aphidius* sp. and *Leptocera* sp. Those species of insects which were confined to ground-level occurred less frequently than those taken at all heights.

3. The insect species collected may be classified into 'aerial' and 'terrestrial' forms according to their vertical distribution, and lists are given of typical species and families in these groups.

4. It was found that the local vegetation determined the general character of the aerial fauna, which showed significant changes from month to month. These changes were generally uniform over the whole front, whether broad or narrow, indicating considerable insect activity over an extensive area, although unevenness occurred, especially at ground-level, owing to the close proximity of breeding places to particular nets.

5. The greatest numbers and variety of insects occurred in May, June and September, times of activity in mating and dispersal. Maximum numbers of most groups occurred at relative humidities below 59 %, wind velocities of 12 m.p.h. and below and at temperatures in excess of 64° F., the latter factor exercising most control.

6. The biological and economic aspects of wind dispersal are discussed particularly in relation to the results of this work in emphasizing the importance of moderate winds and wind drift rather than that of hurricanes and storms. Reference is made to the occurrence of agricultural pest species in the collections.

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REVIEWS

INQUEST ON THE WORLD'S MAMMAL FAUNA

(a) Glover M. Allen (1942). *Extinct and vanishing mammals of the Western Hemisphere, with the marine species of all the Oceans.* American Committee for International Wildlife Protection, Special Publ. No. 11, xv + 620 pp., 24 text drawings.

(b) Francis Harper (1945). *Extinct and vanishing mammals of the Old World.* Ibid., Special Publ. No. 12, xvi + 850 pp., frontispiece and 67 text drawings.
(Address of the Committee: New York Zoological Society, Zoological Park, New York, 60, U.S.A.).

The American Committee for International Wildlife Protection was founded in 1933, and has since published a series of highly valuable surveys of such matters as African game animals, migratory bird protection in North America, the musk-ox population of the Arctic, and on nature conservation generally in the Netherlands Indies, Africa and other countries. The two volumes under review are godsends to the ecologist interested in the fate of the world's mammal fauna, and from their wide scope and lucid treatment ought to be almost equally interesting to anyone concerned with man's influence on wild animals, or with the many rare and peculiar forms included in the monographs.

The authors confine themselves to species that have become extinct within historic or very recent prehistoric times, and they attribute much of, though not all the changes to the action of man either in destroying or altering the habitat of the species, or in directly killing the animals. The historical accounts include such matters as the lion and beaver in Europe, fur trade influences on various species, the cave fossils of the West Indies, and whaling. Altogether some hundreds of species and subspecies are dealt with, the treatment being thorough, scholarly, very well documented (the bibliographies run altogether to over a hundred pages), and with careful attention to taxonomic accuracy. The pleasant drawings by Earle L. Poole, e.g. of such rare forms as *Solenodon* from Hispaniola, though not all original are a useful feature. They give a good impression, and break up the enormous text.

A few of the main points may be selected from this tremendous double compilation.

(a) The Antilles had a specially interesting rodent fauna, most of which became extinct in quite recent times, some of it historically. Remains occur in human kitchen middens, and in owl pellets in caves, of island forms allied to South and Central American types: Echimyids (spiny rats, etc.), large Dinomyids, and Dasyproctids (agoutis). Some still survive, mostly in restricted mountain forest areas. Some very ancient and peculiar insectivores still survive also, such as *Solenodon* in Cuba and Hispaniola. There were (as in South America) some ground sloths that lasted until human

times, and a number of rare and interesting bats, now much reduced by cutting of the forest. On such islands the introduction of rats and mongoose and cats, the advance of agriculture and direct killing by man make the future of these mammal and bird populations very precarious. Similar evidence for birds, in other regions, has been assembled by R. M. de Schauensee (1941, Proc. Acad. Nat. Sci. Philadelphia, 93: 281–324) and E. Mayr (1945, Audubon Mag. 47: 279–82).

Allen's volume surveys also a number of larger forms that have become greatly restricted in range (with the consequent rarity or extinction of certain taxonomic races, though not necessarily of the whole species). The chief of these are the beavers, coypus, chinchillas, martens, fishers, wolves, and wolverines, threatened by fur trade on land; the sea-otter, fur-seals, seals and walruses, threatened by fur trade and hunting in the sea; grizzly bears; various deer, the pronghorn antelope, the bison and musk-ox and mountain sheep; and finally the whales and dolphins.

There are two interesting instances of species diminishing through the loss of their food animals. Prairie range farmers find that ground squirrels and marmots ('prairie dogs') are severe competitors with their stock, and in the last few decades heavy poison campaigns have been carried out to suppress such rodents. The decrease in ground squirrels has affected the prairie 'polecat' (*Mustela nigripes*), which preys on them. Similarly, the buffalo wolf (*Canis lupus nubilus*) is nearly extinct in most areas, because of the decline of the bison.

A great contraction in range of the grizzly bears was inevitable in face of human settlement, though those in Alaska seem to be still numerous, under protection. It is good news that the largest living bear (*Ursus middendorffii*), which lives on Kodiak Island and neighbouring islands in the Aleutians, is no longer in danger. (The author decides that there is not sufficient evidence for the existence of a barren ground bear in Northern Labrador. I have, however, in recent years collected sufficient further evidence from fur trade records to make it more likely that such a bear existed there, at any rate in the last century.)

One finds so many unfamiliar and interesting facts dredged from the literature, that it is difficult to stop mentioning them as illustrations of the strange forms that still exist in the world, the acute need for rational conservation (especially in the British Empire, which comes out not too well from this inquest), and the signs that some countries are beginning to act in time to save quite a number of species. The picture is by no means wholly dark. The sea-otter is safe in California, the Aleutians, the Commander Islands, and probably in the Kuriles. France has made Kerguelen and neighbouring islands into a remote national park partly to conserve the fur-seals. The Pribilof Island fur-seal herds were a million and a half in 1935; and a recent Government report gives 2,700,000 for 1943. The white-tailed deer (*Odocoileus virginianus*) has multiplied amazingly, sometimes to the serious detriment of forests, in areas such as Pennsyl-

vania, where there were said to be some 800,000 in 1939. The guanaco is still abundant; and the vicuna fairly safe, at any rate in Peru. The pronghorn antelope in U.S.A. totalled about 27,000 in 1925, but had risen to about 185,000 by 1939. Many other forms (musk-ox, caribou, mountain sheep, mountain tapir, dugongs and manatees, etc.) can be nursed back if conservation is wisely and consistently applied.

(b) Harper's volume is less easy to summarize in any way, since it contains such enormous masses of reports and notes on individual species and races, without the same amount of general comment as in the other volume. It is, however, prefaced by a concise and interesting review of the state of mammals in the Old World generally, taken region by region. It seems that Europeans are less lethal to mammals at home than they are when they occupy other parts of the world. Europe has only entirely lost six forms (the lion, wild horse, aurochs (*Bos*), Caucasian bison, Pyrenean and Portuguese ibex), though many others have become very scarce and local (bear, wolf, wild cat, beaver, some reindeer, bison, Spanish ibex, the mouflon of Cyprus). We may note, however, that the mouflon (*Ovis musimon*) of Corsica and Sardinia has been successfully introduced into the mountains of Austria, Germany and Hungary, where it has spread and multiplied considerably. The author thinks that Europeans are less hard on predatory mammals than are Americans. But Norway is a marked exception to this generalization; while British game preservers have also heavily depleted our predatory and raptorial fauna.

Asia has not done so badly so far. Indian mammals have been fairly fortunate, Chinese ones less so. The U.S.S.R. has preserved its stocks of the sable in a very large way. But when motor cars and rifles spread more widely in Central Asia the balance may change. The Malay Archipelago also is still rich in mammals, having lost very few entirely. Yet many forms are on the retreat as cultivation and exploitation advance, and will have to be saved by protection. The Netherlands Indies already has (or had) 76 nature reserves in action.

Harper sees Australia and Madagascar as the most vulnerable areas. The Australian mammals have suffered not only from all the usual results of human settlement, exploitation and carelessness, but also from the incursion of European rats, foxes, cats and so forth. Eleven forms are already extinct, and many more on the way. The Tasmanian wolf needs careful preservation. The koala may now get its chance under attempts at protection and management: that such a helpless species could stand up indefinitely to an annual kill for fur running into millions is not to be expected. Madagascar needs tighter protection, especially of the numerous rare and important lemur forms.

Much of the volume concerns animals living on the African continent, and no general summary of this valuable material can be attempted here. The chief absolute losses have been in North and South Africa (which now, however, has in the Kruger National Park one of the finest nature reserves in the world). Many species are contracting their range elsewhere.

It can hardly be doubted that if we are to preserve some of what is left even in reserves or at fairly low densities, much ecological research, leading to experimental wildlife management will have to be done. I think the immediate obstacles are mainly political ones, but that even if political action were to lead to better plans for conservation, enormously more detailed and intricate

knowledge would be required to implement decisions to protect and manage the fauna. The least that can be done is to make sure that information on the subject is widely discussed, and that the modern ideas of wildlife management that are springing up independently everywhere are given world-wide circulation. Some organization for this purpose for the British Empire, but with a world basis of knowledge, is urgently needed. These two fine volumes provide essential material towards such a world survey.   CHARLES ELTON

CONSERVATION PLANS FOR BRITAIN

(a) John Dower (1945). *National Parks in England and Wales*. Ministry of Town and Country Planning. 57 pp., 2 maps. (H.M. Stationery Office, London. Cmd. 6628.) Price 1s.

(b) [J. D. Ramsay and others] (1945). *National Parks: a Scottish survey. Report by the Scottish National Parks Survey Committee*. Dept. of Health for Scotland. 27 pp., 1 map. (H.M. Stationery Office, Edinburgh. Cmd. 6631.) Price 6d.

(c) A. G. Tansley (1945). *Our heritage of wild nature. A plea for organized nature conservation*. 74 pp., 26 photographs. Cambridge: (Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1). Price 7s. 6d.

(a) Ecologists are deeply affected by conservation at all levels, whether it be on small patches of land preserved by naturalists or private societies, in national nature reserves, within scheduled conservation areas protected from extreme industrial or urban development, or in full-blown national parks. For it is chiefly within such harbourage that the remnants and traces of former natural and semi-natural plant and animal communities have a real prospect of survival, and the ecologist can look far ahead in planning his surveys and experiments.

We are going to be a poor country for some years. At the same time science and engineering offer the means of intensive exploitation of all our natural resources. Increased draining, quarrying for cement materials, surface coal and iron ore mining, improved hill pasturing, ploughing of marginal land, conifer afforestation, wider roads and bigger aerodromes, housing estates, and military training areas will heavily threaten both our wildlife and the recreational outlets for our townspeople. The problem of the top planner is to reconcile immediate and necessary material development of land with its use for science and recreation in the widest cultural sense (which implies continuation in some areas at least of the types of land use or non-use that give our country its traditional charm, its vegetation and other wild life, and its scientific interest generally).

Mr Dower's Report, brilliantly arranged and lucidly written, adds to a series of recent White Papers that are absorbing to read because they analyse and discuss live problems in an authoritative way. He recommends for a first instalment of National Parks the Lake District, Snowdonia, Dartmoor, the Peak District and Dovedale, the Pembrokeshire coast, and parts of the Cornish coast— a total of about 2300 square miles. These, he suggests, should be followed by a further instalment with the Craven Pennines, some southern Welsh hills (the Black

Mountains and Brecon Beacons), Exmoor and the north Devon coast, and the Roman Wall in the north of England—some 1300 square miles in all. This is not all. Twelve further areas (including the Norfolk Broads, Dorset coast and heaths, some Downland, and hill-lands in the North and in Wales) are listed as reserve areas for possible further National Parks, as well as a number that require some restrictions on development. Two maps summarize these plans.

I cannot even notice here the many points raised in his discussion of conflicting interests and the best administrative compromise for the secure control of National Park objectives. But two general points ought to be mentioned. First, National Parks in Britain cannot in themselves be dedicated solely as wildlife reserves: our land is too small, crowded and occupied by existing land usage for any but small areas to be set aside for this purpose. The second point is that agricultural and many other rural or semi-rural industries will occupy large parts of the Parks and rightly continue to do so. It is no sterilization of rural areas that is proposed, but rather the preservation and harmonious development of land use up to limits set by the natural features whose conservation, enjoyment and study are desired.

These special characteristics of the English problem imply a corresponding intensification of wildlife conservation in smaller nature reserves and also over the country generally. Mr Dower gives consideration to the needs of natural conservation (paras. 60–68). He supposes that the National Parks Authority (which he visualizes in some connexion with the Minister of Town and Country Planning) would set aside some areas within National Parks as nature reserves, and might also be charged with the administration of other National Nature Reserves outside the Parks. There would also be a number of local reserves run by other bodies. He also proposes another Government body called, say, the Wild Life Conservation Council, which would *advise* the Authority how to run not only the Reserves, but also wildlife generally within the Parks.

These plans differ somewhat from those proposed by the British Ecological Society in recent reports, and they rather seem to miss the point that National Nature Reserves will be the main ecological source and sustenance of the Wild Life Council's surveys and research and therefore would far better be under direct scientific management by such a Council. However, these are matters to be studied by the new Government Committee on National Nature Reserves, on which ecology is strongly represented. The great thing is that this fine Report puts not only National Parks but national nature conservation on the Government map. Furthermore, the author is optimistic, for he says in the first sentence: 'National Parks, as one of the major objectives of postwar town and country planning, rest on a firm basis of popular desire, informed opinion and Ministerial approval.... It may be assumed that the case, in broad principle, has already been made and won.'

(*b*) The hard-worked proverbial Martian or other foreign visitor might think is fairly nonsensical that an island whose area is only about 89,000 square miles should submit to having its recreation areas and wildlife conservation planned by two separate lots of people, who seem to take practically no notice of one another. The motorist, the fisherman, the bird-watcher, the purple sandpiper or short-eared owl, or the seeds of *Epilobium angustifolium* (or indeed the 2½*d.* post or the Agricultural Research Council) carry out their activities both in Scotland and in England and Wales. National Parks and nature reserves have their own human population equilibria that are vital factors in successful planning of access and use.

The general part of the Scottish Report is business-like to the point of bareness. But the recommendations are solid and encouraging, and cover areas of extreme ecological interest: an immediate instalment of five large National Parks in the regions of Loch Lomond, Ben Nevis, the Cairngorms, and (north of the Caledonian Canal) Glen Afric and Loch Torridon. Following these are reserve areas for future Parks in the regions of Moidart, Ben Lawers and St Mary's Loch. These two groups cover 1870 and 730 square miles respectively.

Nature conservation has brief encouragement: some nature reserves inside these Parks, also outside them (as on the lower reaches of the Garry and Moriston, and the Black Wood of Rannoch). There is a warning that reserves must not be allowed to become breeding centres for agricultural pests. The most interesting scientific notes come in the detailed specifications of each Park area, which are much fuller than in the English Report.

(*c*) Thoreau wrote that 'We need to witness our own limits transgressed, and some life pasturing freely where we never wander'. Wildlife is not only a pleasure, a resource or an intellectual problem. Given a reasonable chance, it simply exists and abounds in its own extraordinary variety and rhythm, whether we write about it, eat it, try to measure its pulse—or not. Thoreau also said: 'At the same time that we are earnest to explore and learn all things, we require that all things be mysterious and unexplorable, that land and sea be infinitely wild, unsurveyed, and unfathomed by us because unfathomable.' But this was written ninety years ago, before we had seriously begun to scramble together the floras, faunas and diseases of the continents, finish 'settling' in the northern deciduous forest belt, farm the sea with mechanically driven ships and gear, hunt whales with radar, discover insect and mammal poisons of undreamed of toxicity, or become both numerous and educated enough to require large volumes of cubic space to live in and travel on. Man is now a pervading ecological force, and the only way he can conserve even modified natural plant and animal communities is by taking direct responsibility for their survival, scientifically investigating their environment and populations, and framing policies of management, if not for every species (of course, an impossibility), at any rate for the habitats and most influential forms (including himself).

Prof. Tansley, in this very attractive and interesting book, reviews the whole problem of conserving our native (and established alien) vegetation and animal life, which he sensibly includes all together under the general term 'wild life', much of which he recognizes, however, to be only semi-natural in its community balance.

I do not know any book on ecology and conservation that has quite the qualities of this one: authoritative on the dynamic ecology of plant communities and well-informed about the British rural scene, equally aware of the special problems of animal populations, stating with massive wisdom the different values of material development, science, education, humaneness and enjoyment of rural beauty, and bringing the threads together into a lucid exposition of practical policy for Government action.

The concise account of vegetation types (with good photographs) is based on the author's larger work on *The British Islands and their Vegetation*. Only a few

special points can be selected here. Our commons are mostly regressive woodland. 'Today our oakwoods are economically almost worthless', and often not regenerating. Beech is flourishing, but needs selective instead of clear felling, if the flora and fauna is to survive. Selective felling is also desirable for the Forestry Commission's conifer forests. The primeval pine woods of Scotland are much endangered by fellings. 'Improved' sheep grazings might injure the downland flora. Much heathland, from its light soil, is chosen for building sites.

Wild animal life is discussed, and illustrated by some excellent mammal photographs. Its conservation is shown to require not only Nature Reserves, but a wild life Service to help the country generally. In the discussion of policy, Prof. Tansley follows the Report already drawn up for our Society under his chairmanship ('Nature Conservation and Nature Reserves', published in the *Journals of Ecology* and *Animal Ecology*, 1944, and also issued separately) and the 'Memorandum on Wild Life Conservation and Ecological Research from the National Standpoint' (issued separately, 1945). These need not be summarized in detail here. They envisage Government responsibility for wild life conservation shouldered by a new Ecological Research Council (under the Privy Council as Government Department) which would control a Wild Life Service and a chain of nature reserves. It should be mentioned here also, that the Nature Reserves Investigation Committee, an *ad hoc* body set up by a group of organizations in 1942, has also presented some very valuable ideas about the same problems (*Nature Conservation in Great Britain*. Society for the Promotion of Nature Reserves, 1945). Since Prof. Tansley in his book discusses the proposals of this Committee very thoroughly, it will not be further considered here. But its work and conclusions are of first-rate importance.

Prof. Tansley has done ecologists as well as the general public a considerable service by devoting his leisure years to focusing the conservation problem, which is now properly recognized as a serious aspect of future planning.

CHARLES ELTON

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3s. 6d. per annum post free (in two sets, May and November).

Abstracting has been done voluntarily by H. F. Barnes, D. Chitty, C. Elton, R. B. Freeman, B. M. Hobby, F. T. K. Pentelow, H. N. Southern and H. V. Thompson.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

CONTENTS

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(a) MARINE AND BRACKISH

Phillips, S. (1944). 'Observations on the marine biology of Feock on the Fal.' Rep. R. Cornwall Polyt. Soc. 11: 89–111.

A study, with species list, of an estuarine shore and shallow-water environment. The fauna is compared with that of St Ives on the north Cornish coast. The list is particularly rich in Collembola and in Acari.

McMillan, N. F. (1944). 'The distribution of *Monodonta* (*Trochus*) *lineata* (da Costa) in Britain.' Northw. Nat. 19: 290–2.

This littoral mollusc occurs from Dorset to Caernarvon and Anglesey and along the Irish shores though scarce in the north and east.

(b) FRESH WATER

Underdown, H. C. (1945). 'Birds of the riverside.' Salm. Trout Mag. Lond. No. 114: 156–7.

A popular account of the appearance and habit of the reed bunting (*Emberiza schoeniclus*).

Went, A. E. J. (1944). 'Notes on some Irish char.' Irish Nat. J. 8: 202–5.

Records of *Salvelinus colii* from Lough Mask (Co. Mayo) and Waterville river (Co. Kerry) and *S. scharffi* from Lough Ennell (Co. Westmeath). The latter was only known previously from a single specimen from a neighbouring Lough.

Went, A. E. J. (1945). 'The distribution of Irish char (*Salvelinus* spp.).' Proc. R. Irish Acad. B, 50: 167–89.

Compilation of records for all six species of Irish char.

Sawyer, F. E. (1945). 'Two British spurwings: the habits and appearance of *C. pennulatum* and *C. luteolum*.' Salm. Trout Mag. Lond. No. 114: 150–5.

How to distinguish, by appearance and habit, the two British species of *Centroptilum* (Ephemeroptera) from each other and from species of *Baëtis*.

Halbert, J. N. (1945). 'List of Irish fresh-water mites (Hydracarina).' Proc. R. Irish Acad. B, 50 (4): 39–104.

218 species including new genera and species.

Černosvitov, L. (1945). 'Oligochaeta from Windermere and the Lake District.' Proc. Zool. Soc. Lond. 114: 523–48.

A useful list with discussions upon systematics and distribution.

(c) Land

Melmore, S. (1944). 'A statistical analysis of the flesh measurements.' In **Kirk, J. C. & Wagstaffe, R. (1944).** 'A contribution to the study of the Scottish wild cat. Pt. 1 (cont.).' Northw. Nat. 19: 14–23.

Contains considerable discussion of the methods used.

Hartridge, H. (1945). 'Avoidance of obstacles by bats.' Nature, Lond. 155: 55.

The original hypothesis that the reflexion of high-pitched sounds enables a bat to detect obstacles arose from observations in Cambridge.

Rollin, N. (1945). 'Song-thrush song.' Brit. Birds, 38: 262–70.

The total amount of time during the day used in singing is compared for birds at different stages of the breeding cycle. Unmated birds sang most, and analysis for one individual showed that 41 % of the 24 hr. was spent in singing and only 21 % was left for feeding and other daytime activities.

Owen, J. H. (1945). 'The nesting of the long-tailed tit.' Brit. Birds, 38: 271–3.

Of 70 nests found, 35 were built in blackthorn bushes. Many other details are given on nest building, mortality of young, etc.

Mason, A. G. (1944). 'Combat display of the corncrake.' Irish Nat. J. 8: 200–2.

Chambers, V. H. (1945). 'British bees and wind-borne pollen.' Nature, Lond. 155: 145.

Some pollen loads of *Andrena* spp. had been almost entirely collected from anemophilous flowers such as *Quercus* or *Castanea*.

Butler, C. G. (1945). 'The influence of various physical and biological factors of the environment on honeybee activity. An examination of the relationship between activity and nectar concentration and abundance.' J. Exp. Biol. 21: 5–12.

Bees visit those species with the highest concentration of nectar (which may vary hourly, probably due to changes in humidity). The abundance of nectar appears to determine the proportion of foraging bees which will be able to work a given species of flower.

Niblett, M. (1945). 'British gall-causing Cynipidae. IV.' Entomologist, 78: 72–4.

Records the breeding of the Chalcid *Synergus evanescens* from stunted acorns. This species hitherto was known only as an inquiline infesting galls of the Cynipid *Andricus fecundatrix*. The suggestion is made that the ovipositing parent *Synergus evanescens* mistakes the young acorn for a young *fecundatrix* gall, to which it has some resemblance. The proof that *Andricus occultus* and *A. solitarius* are alternating generations of the same species is also given.

Benson, R. B. (1945). 'Sawflies represented in the mainland of Britain by two races (Hym., Symphyta).' Ent. Mon. Mag. 81: 103–5.

In each case the southern of the two races is associated with the European deciduous forest zone and the northern race with the taiga, the boreal coniferous forest zone. This taiga zone in its western outliers in Scotland represents but an impoverished Atlantic phase, mostly birch forest, moor and bog, and its fauna, or at least its sawfly fauna, bears clear indications of a similar affinity with the Eurasian taiga, just as our mountain-top fauna contains species belonging to the Arctic and Alpine tundra. The presence, then, in the mainland of Britain of two races of sawflies is perhaps due to the same causes that give two main types of climatic-climax forest in Britain. The history of these sawfly races is possibly bound up with that of the forests.

Collenette, C. L. (1945). 'Orientation experiments on larvae of *Pieris brassicae* L.' Entomologist, 78: 33–6.

Experiments seem to show that the larvae cannot see distinctly at a distance, or that they are unable to recognize their food-plant by sight. When the light is good enough (sun or light cloud), they make for the nearest object above their own level which looms over them, and up to 2 ft. distant.

Praed, C. W. Mackworth (1945). 'Three seasons in the Western Highlands (Lep., Odon., Col.).' Ent. Mon. Mag. 81: 114–17.

The butterfly *Carterocephalus palaemon* recently discovered in this district is at least biologically a distinct race from that of the eastern counties of England, and appears also to be distinct in colouration. Its appearance on 10 May in 1942, and on 28 May in the cold, wet season of 1943, is a month earlier than is normal with the English race. Its coloration is cleaner and harder, with no yellow wash on the underside. Its food plant must be different: *Molinia* is suspected, as neither *Brachypodium* nor *Bromus* occurs in the district. It is notable as being the only butterfly to fly regularly in rain, and its habitat is varied, either dry grassy banks, or glades in wet woods full of bog myrtle. Other Lepidoptera, Odonata and a few beetles are also discussed.

Bacon, A. F. L. (1945). '*Hamearis lucina* in open country.' Entomologist, 78: 93.

The Duke of Burgundy fritillary found in some numbers on an open down. The standard text-books all associate it with woods.

Dancy, T. A. & Savage, L. E. (1945). 'Noctuae captures in mid-Sussex from the yew hedges.' Ent. Rec. 57: 58–9.

A sugary excretion from a scale insect on the small twigs of a yew hedge attracted sixty-six species of Noctuid moths in the period 1943–4.

de Worms, C. G. M. (1945). 'Further notes on *Oria musculosa* in the Salisbury district.' Entomologist, 78: 65–6.

This moth is a potential menace to cereal crops in this country under wartime conditions of agriculture.

Kettlewell, H. B. D. (1945). 'The life-history of *Oria musculosa* in Britain (Lep. Agrotidae).' Entomologist, 78: 85–6.

Believes that the main reservoir of this insect will be found outside cultivated areas and that the larvae feed more usually though less obviously in the various grasses bordering the fields.

Henderson, J. L. (1945). 'The beetles of a suburban London garden in Surrey.' Ent. Mon. Mag. 81: 63–6.

A list of 321 beetles taken in two seasons in a loosely built-up area of forty years' standing.

Kevan, D. K. (1945). 'The Coleoptera of an Edinburgh garden.' Ent. Mon. Mag. 81: 112–13.

Records of 165 species of beetles taken during 1943 and 1944 in a normal city garden with sizable lawn and borders, but no uncultivated portion.

Duffy, E. A. J. (1945). '*Dorytomus taeniatus* F. (Col., Curculionidae) reared from sallow catkins.' Ent. Mon. Mag. 81: 10.

Reynolds, J. M. (1945). 'On the inheritance of food effects in a flour beetle, *Tribolium destructor*.' Proc. Roy. Soc. B, 132: 438–51.

Parental feeding affects the rate of development and mortality of the offspring. Larvae developed more rapidly on an inferior food if their parents had been well fed than they did on good food if their parents had had inferior food.

Fisher, R. C. (1945). 'Wood-boring insects in beech furniture.' Nature, Lond. 155: 116.

Beech furniture is not normally attacked by *Lyctus* or *Xestobium* (even *X. rufovillosum*, the death-watch beetle, chiefly attacks structural timbers). The common furniture beetle (*Anobium punctatum*) is the most frequent cause of 'worm' in furniture.

Allen, A. A. (1945). '*Globicornis nigripes* F. (Col., Dermestidae) rediscovered in Windsor Forest and reinstated as British.' Ent. Mon. Mag. 81: 84–5.

Two specimens taken by sweeping grass under oaks. Stephens recorded the insect from near Windsor over a hundred years ago. The only other record in the intervening period is a doubtful one from Tewkesbury.

Roebuck, A. & Bray, S. P. V. (1944). 'The effect of altitude on the distribution of Eláteridae in grassland in Derbyshire.' Northw. Nat. 19: 47–50.

Species of the genus *Agriotes* are largely predominant in lowland fields, but their predominance decreases with increasing altitude. They are replaced mainly by *Corymbites*. The absolute numbers of all species combined also decreases with altitude.

Allen, A. A. (1945). 'A note on *Aromia moschata* L. (Col., Cerambycidae).' Ent. Mon. Mag. 81: 37.

Suspects that the musk beetle is now much more local and restricted than formerly. Suggests that it may be a stem-miner rather than an inhabitant of decaying and rotten trunks of willows.

Duffy, E. A. J. (1945). 'Observations on *Aromia moschata* L. (Col., Cerambycidae).' Ent. Mon. Mag. 81: 87–8.

This insect was found freely on slender branched bushes of *Salix atrocinerea*, but not on old rugged willows.

Stephens, J. A. (1945). '*Aromia moschata* L. (Col., Cerambycidae) associated with sound willows in Kent.' Ent. Mon. Mag. 81: 88.

The musk beetle does not live in rotten or very decayed trees, but in willows in a sound state or just beginning to decay.

Massee, A. M. (1945). '*Aromia moschata* L. (Col., Cerambycidae).' Ent. Mon. Mag. 81: 88.

The musk beetle bores into the main trunks of willows and does not feed in the stems of the tree.

Sankey, J. H. P. (1945). 'Observations on *Pentatoma rufipes* L. (Hem., Pentatomidae) on cherry trees.' Ent. Mon. Mag. 81: 86–7.

This bug showed a preference for certain varieties of cherries. It hibernates in the second instar on the lower parts of trees where there is suitable shelter.

Morley, C. (1945). 'Diptera in winter.' Ent. Mon. Mag. 81: 99–100.

Species of 18 families were taken on windows of a house in Suffolk between 20 October and 20 December 1944.

Cragg, J. B. & Ramage, G. R. (1945). 'Chemotropic studies on the blow-flies *Lucilia sericata* (Mg.) and *Lucilia caesar* (L.).' Parasitology, 36: 168–75.

Oviposition occurred in response to certain chemicals on moist fleece, i.e. did not entirely depend on some factor produced by the living animal.

Milne, A. (1945). 'The ecology of the sheep tick, *Ixodes ricinus* L. Host availability and seasonal activity.' Parasitology, 36: 153–7.

It had been suggested that the end of heavy tick infestation in spring came only because all the ticks were gorged. Sheep were therefore withheld from a grazing so that the ticks would be short of food until later in the season. However, the peak of female tick activity was not prolonged into the summer: activity finished when over half the females were still unfed.

Milne, A. (1945). 'The ecology of the sheep tick, *Ixodes ricinus* L. The seasonal activity in Britain with particular reference to Northern England.' Parasitology, 36: 142–52.

There are usually two peaks of female activity each year: in spring and autumn. Among the factors of the microclimate, humidity is probably of great importance in controlling this seasonal incidence.

Collinge, W. E. (1944). 'Notes on the terrestrial Isopoda (woodlice). No. IX.' Northw. Nat. 19: 5–14.

Contains notes on dispersal; the distribution of the two species of the genus *Porcellionides*, *pruinosus* largely confined to greenhouses and gardens, and *cingendus* from coastal areas in the south-west; and the breeding of *Ligidium hypnorum*.

Collinge, W. E. (1944). 'Notes on the terrestrial Isopoda (woodlice). No. X.' Northw. Nat. 19: 112–23.

Contains notes on duration of life, behaviour of *Armadillidium vulgare* in captivity, cannibalism, reactions to temperature, climbing habits, and distribution of the seven British species of *Armadillidium*.

Collinge, W. E. (1944). 'Notes on the terrestrial Isopoda (woodlice). No. XI.' Northw. Nat. 19: 231–8.

Contains notes on the distribution of the seven British species of *Trichoniscus* and three of the species of *Porcellio*.

Ellis, A. E. (1945). '*Limax flavus* L. in a "wild" habitat.' J. Conch. 22: 135.

Record from the foot of Babbacombe Cliffs, Devon, an apparently 'wild' habitat for this species which normally lives in close association with man.

Phillips, S.-M. (1944). 'Some preliminary observations on the aggregation of certain molluscs.' Northw. Nat. 19: 280–4.

Milax sowerbyi was found to congregate under experimental dry conditions, the smaller surface delaying desiccation. Observations on other land molluscs in the wild are given.

(d) SMALL ISLANDS

Harrison, J. W. Heslop (1945). 'Remarks on certain Lepidoptera from the Western Isles of Scotland.' Entomologist, 78: 18–21.

Distributional records with some ecological data.

Harrison, J. W. Heslop (1945). 'Further observations on the genus *Zygaena* in the Inner and Outer Hebrides.' Ent. Rec. 57: 25–7.

Discusses *Z. filipendulae*, *Z. purpuralis* and *Z. achilleae*.

Beirne, B. P. (1945). 'The Lepidoptera of Shetland.' Ent. Rec. 57: 37–40.

A useful compilation in which attention is specially directed to species requiring confirmation.

Alexander, W. B. *et al.* (1945). 'Observations on the breeding birds of Lundy in 1942.' Brit. Birds, 38: 182–91.

The main part of this paper is summarized in a table, which gives the status of all the land species at various intervals between 1922 and 1942.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Duncan, F. Martin (1943). 'A simple method for the microscopic examination of mammalian hairs, with special reference to the cuticular scales.' J. R. Micr. Soc. 63: 85–8.

van Emden, F. I. (1945). 'Larvae of British beetles. V. Elateridae.' Ent. Mon. Mag. 81: 13–37.

Keys for the identifications of wireworms.

Cooper, B. A. (1945). 'Notes on certain Elaterid (Col.) larvae.' Ent. Mon. Mag. 81: 128–30.

Gives figures and couplets for separation of larvae of *Corymbites incanus*, *Limonius aeruginosus* and *L. minutus* and *Agriotes pallidulus*.

Kevan, D. K. (1945). 'The aedeagi of the British species of the genus *Catops* Pk. (Col., Cholevidae).' Ent. Mon. Mag. 81: 69–72.

Includes key and figures of the genitalia.

Kevan, D. K. (1945). 'The aedeagi of the British species of the genera *Ptomaphagus* Ill., *Nemadus* Th., *Nargus* Th. and *Bathyscia* Sch. (Col., Cholevidae).' Ent. Mon. Mag. 81: 121–5.

Keys and figures of the genitalia.

Collin, J. E. (1945). 'The British species of Opomyzidae (Diptera).' Ent. Rec. 57: 13–16.

Key to British species.

Keilin, D. (1944). 'Respiratory systems and respiratory adaptations in larvae and pupae of Diptera.' Parasitology, 36: 1–66.

The enormous range of habitat in which dipterous larvae occur makes them peculiarly suitable for a study of different evolutionary trends. This paper is part of a very comprehensive study.

Collinge, W. E. (1944). 'On the British species of the Isopod genus *Asellus* (Geoffroy).' Northw. Nat. 19: 44–7.

Lowndes, A. G. (1945). 'The displacement method of weighing living aquatic organisms.' Nature, Lond. 155: 520–1.

Discusses some of the fundamental applications of accurate knowledge about weight and density of living organisms.

3. PARASITES

O'Mahony, E. (1945). 'A scarce Irish beetle, *Leptinus testaceus* Müll. (Col., Leptinidae).' Ent. Mon. Mag. 81: 6.

Nest of wood-mouse (*Apodemus s. sylvaticus*) at Whitestown, Tallaght, Co. Dublin, 28 October 1944, yielded 25 fleas (*Ctenophthalmus agyrtes nobilis*), 41 mites (*Laelaps* sp.) and 17 specimens of the blind parasitic beetle *Leptinus testaceus*.

Unsworth, K. (1944). 'Observations on the life-cycle of a species of *Diphyllobothrium* found parasitizing trout in Great Britain.' Ann. Trop. Med. Parasit. 38: 213–19.

An unknown species of cestode very similar to *D. latum* was heavily infesting trout in reservoirs. Its adult stage occurs in a mammalian host. Successful experimental transmissions were made: plerocercoids from trout infested a rat; eggs from the rat's faeces were fed to copepods which were fed to sticklebacks which were fed to pike. Finally plerocercoids from either stickleback or pike were found to infest puppies.

Sproston, N. G. (1944). '*Ichthyosporidium hoferi* (Plehn and Mulsow, 1911), an internal fungoid parasite of the mackerel.' J. Mar. Biol. Ass. U.K. 26: 72–98.

Causing a fatal disease among mackerel in British waters, this fungus needs no intermediate host, as growth of its resting bodies occurs in the mackerel. Previous descriptions of similar growth forms are reviewed, as is also the effect of the disease on mackerel as a commodity.

Rees, G. (1945). 'A record of parasitic worms from fishes in rock pools at Aberystwyth.' Parasitology, 36: 165–7.

Seven species of nematodes, three of cestodes, two of nematodes and two of Acanthocephala were taken from four species of fish. Eleven of these are new host records.

Bryden, J. W. & Bishop, M. W. H. (1945). '*Perilitus coccinellae* (Hym., Braconidae) in Cambridgeshire.' Ent. Mon. Mag. 81: 51–2.

This parasite was bred from the ladybird *Coccinella septempunctata*; unsuccessful attacks were made on *Propylea quatuordecimpunctata*, *Adalia bipunctata* and *Thea vigintiduopunctata*. It is capable of thelytokous parthenogenesis. A footnote by Dr K. G. Blair confirms breeding from *C. septempunctata* and adds *C. undecimpunctata* as a host.

4. FOOD AND FOOD HABITS

Tucker, B. W. (1944). 'The ejection of pellets by passerine and other birds.' Brit. Birds, 38: 50–2.

A preliminary list with authorities is given of species known to produce the indigestible parts of their food as pellets.

Scott, A. D. (1945). 'Blue titmouse feeding on bees.' Ent. Mon. Mag. 81: 46.

It is not unusual for a blue tit to eat honey-bees, at least during periods when other food is scarce.

Glegg, W. E. (1945). 'Fish and other aquatic animals preying on birds.' Ibis, 87: 422–33.

A collection of instances, mostly from literature, where birds have been seen to be attacked by fish or mammals.

O'Rourke, F. J. (1945). 'Method used by wasps of the genus *Vespa* in killing prey.' Irish Nat. J. 8: 238–41.

The mandibles are more important than the sting in killing insect prey. Usually the head is removed and often the wings and legs.

Massee, A. M. (1945). '*Laemostenus terricola* L. (Col., Carabidae) feeding on stored apples.' Ent. Mon. Mag. 81: 9.

The damage was done in a cellar at Holt Wood, Aylesford, Kent. Only dessert apples were attacked, not culinary apples in the same store. Soft brown rots set in where the beetles have been feeding and the fruits readily decay.

5. POPULATION STUDIES

Brambell, F. W. Rogers (1944). 'The reproduction of the wild rabbit *Oryctolagus cuniculus* (L.).' Proc. Zool. Soc. Lond. 114: 1–45.

An important paper containing the complete results of the investigation into pre-natal mortality in the rabbit, as well as a general survey of reproduction in this species as seen in a large sample from Caernarvonshire. The high uterine mortality (50–60 % of litters are lost about the 12th to 14th day of pregnancy) previously described is confirmed by further data. Since during the intensive part of the breeding season (Jan.-June) reproduction is practically at full pressure, and new litters are conceived immediately after the previous one is born or absorbed, and also since breeding starts very suddenly, a series of waves of productivity at fortnightly intervals is set up in the population. The onset of breeding is controlled by the condition of the females, the cessation by that of the males. There are many other valuable data and discussions.

Deanesly, R. (1944). 'The reproductive cycle of the female weasel (*Mustela nivalis*).' Proc. Zool. Soc. Lond. 114: 339–49.

Of the 126 specimens, on which this study is based, 78 came from Caernarvonshire. The breeding season extends from March to August and probably many second litters are born. Young were first taken in the traps in June and from July they much outnumbered the adults. Several cases were recorded of young females breeding in their first summer.

Lack, D. (1944). 'Ecological aspects of species-formation in passerine birds.' Ibis, 86: 260–86.

This paper centres round a theoretical discussion of the possible results, when two closely related species, having differentiated in geographical isolation, are brought together again. Competition must ensue and ecological may often follow morphological differentiation. This contention is examined in the light of the ecology and distribution of closely related groups among British passerines (there is other evidence from non-British forms). The commonest result is differentiation of habitat, the next commonest the development of size differences (presumably indicating different food), while there are a number of still unexplained cases of apparent overlap.

Alexander, W. B. & Lack, D. (1944). 'Changes in status among British breeding birds.' Brit. Birds, 38: 42–5, 62–9, 82–8.

A survey, largely from the last hundred years, of increases and decreases in the populations of British birds. Of all species reviewed, 47 show increase, 48 decrease, 21 have decreased and then increased again and 57 show no change. Of the increase, 30 have probably been uninfluenced by human activity, but of the decreases only 15.

Southern, H. N. & Tucker, B. W. (1944). 'The Manx shearwater on Lundy.' Brit. Birds, 38: 122–9.

Puffinus puffinus has been known to frequent Lundy for over 100 years, but breeding has only infrequently been proved. Investigations in 1942 showed that, although some scores of birds were coming to land each night, very few were nesting. One nest only was found, although a number of burrows were occupied by pairs of birds, which may have been immatures.

Alexander, W. B. (1945). 'The index of heron population, 1944.' Brit. Birds, 38: 232–4.

The year 1944 showed an increase of about 12 % in the heron breeding population, restoring the index to 92 % of the original datum established in 1927. A graph covering the whole period shows a marked correlation with winter temperature. The quickness of recovery after a cold winter suggests that herons may breed in their first year.

Norris, C. A. (1945). 'Summary of a report on the distribution and status of the corncrake (*Crex crex*).' Brit. Birds, 38: 142–8, 162–8.

This summary, largely prepared by W. B. Alexander, shows that the decrease of this species in the British Isles has proceeded from a south-eastern direction towards the north-west. An area from north of the Humber to Glamorgan has only sporadic pairs left; a small area consisting of north-west Ireland, the western Scottish islands, Orkney and Shetland still has undiminished numbers; the intervening area shows variation, but generally is marked by considerable decrease.

Bell, J. J. H. (1945). 'Some observations on the winter flocks of the starling.' Trans. Herts. Nat. Hist. Soc. Fld. Cl. 22: 99–101.

Observations on flock size, relation to dusk and dawn, and various points of flock behaviour, of flocks of the starling moving between roosting and feeding grounds.

Went, A. E. J. (1945). 'Irish previously spawned salmon.' Sci. Proc. R. Dublin Soc. 24: 1–8.

Of the salmon ascending Irish rivers about 5 % have spawned once and 0·05 % twice before.

Farran, G. P. (1944). 'The herring fishery in Eire, 1921–1941.' J. Dep. Agric. Eire, 41: 229–62.

A survey by areas of the annual and seasonal catch of herrings. The supply is least in March, greatest in May and June.

Popham, E. J. (1944). 'A study of the changes in an aquatic insect population, using minnows as predators.' Proc. Zool. Soc. Lond. 114: 74–81.

A pond containing three species of the Corixid *Sigara* had 50 minnows (*Phoxinus*) introduced into it. At the end of a week the proportion of specimens of all three species closely adapted to the colour of the environment had increased markedly.

Walsh, G. B. (1945). 'Causes of abundance or scarcity of wasps (Hym., Vespidae).' Ent. Mon. Mag. 81: 89.

Figures from Llandudno lend good support to the view that in years in which the rainfall during April, May and June is low wasps tend to be abundant in the summer and autumn, though figures for Scarborough are less in favour of the theory.

Scott, H. (1945). 'Rainfall in relation to scarcity or abundance of wasps (Hym., Vespidae).' Ent. Mon. Mag. 81: 97–8.

In Henley the winter season 1942–3, preceding a summer when wasps were very scarce, showed several very wet months, October, December and an exceptionally wet January: while, though March and April, 1943, were much drier than the average, May was wetter. On the other hand, in the winter 1943–4, preceding a summer with abundance of wasps, all the months except October were below the average and some very much so, while the rainfall continued scanty through the summer of 1944.

Robertson, F. W. & Sang, J. H. (1944). 'The ecological determinants of population growth in a *Drosophila* culture. I. Fecundity of adult flies.' Proc. Roy. Soc. B, 132: 258–77.

An important paper on the relationship between quantity and quality of the food (yeast), crowding, and egg production. Decrease in fecundity was found to take place only as a result of competition for food and not simply from the crowding of adults. Little competition occurred for oviposition space.

Robertson, F. W. & Sang, J. H. (1944). 'The ecological determinants of population growth in a *Drosophila* culture. II. Circumstances affecting egg viability.' Proc. Roy. Soc. B, 132: 277–91.

Eggs laid on the second day of adult life are formed from food reserves accumulated in the larval stage. They are less viable than those laid on the third to fifth days, and after this again viability is less. About 40 % of the eggs laid in the first 10 days fail to hatch. Both fecundity and egg viability can be affected by the same change of diet, egg viability being the more sensitive.

Jacob, F. H. (1944). 'A two years' survey of the potato aphides in the Northern Agricultural Advisory Province.' Ann. Appl. Biol. 31: 312–19.

Population studies in Northumberland, Durham, Cumberland and Westmorland with special reference to overwintering and the prevailing weather conditions at the time of the spring migration.

Arthur, D. R. (1945). 'A note on two Braconids (Hym.) in their control of corn aphides (Hem.).' Ent. Mon. Mag. 81: 43–5.

In South Wales, 1942–4, the most important factors in the biological control of the corn aphides *Macrosiphum granarium*, *Aphis avenae* and *Myzus festucae* were the Braconids *Aphidius avenae* and *A. granarius*. The peak of parasite activity of *A. granarius* was reached between 21 and 30 May with a parasitism of 68%, that of *A. avenae* was some 7–10 days later with parasitism of 67%. There was then a gradual slowing up of parasitism and by the end of July and early August the number of aphides present was negligible. Owing to (*a*) the respective rates of reproduction of aphides and parasites and (*b*) the reproduction of aphids parasitized after the third instar, the Braconid species were unable to exercise maximum control until the aphide population had passed through several generations and been responsible for some damage to the crop. Alate aphides are less susceptible to parasitism than apterous forms. Under experimental conditions *A. avenae* was superior to *A. granarius* in parasitizing apterous forms of *Myzus festucae*, but no significant differences were observed in their attacks on the other species.

Advisory Entomologists' Conference (1944). 'Wireworms and food production. A wireworm survey of England and Wales 1939–1942.' Bull. Minist. Agric. Lond. No. 128: 1–62. (H.M. Stationery Office, London. Price 1*s.*)

Wireworms live in grassland and are not a serious pest until the grass is ploughed up. Under arable farming they decrease in density each year but may do serious damage in the first years. A technique of sampling was designed so that farmers could be advised which crops to grow. Peas, beans, flax and linseed will succeed even where there are over a million wireworms per acre. Barley is a better risk than other cereals; but potatoes should only be grown where fields are in the low population group of less than 300,000 wireworms per acre.

The wireworm population is highest in the east and south, particularly in heavy soils.

Miles, H. W. (1945). 'Wireworms and food production.' Nature, Lond. 155: 136–8.

A review of the official bulletin of the same title.

Jones, J. R. Erichsen (1944). 'The Elaterid population of mid- and West Wales.' Proc. Zool. Soc. Lond. 114: 350–9.

Samples from 1871 fields showed an average density of 218,000 per acre: less than 10% had densities from 600,000 to 1 million. There is a slight tendency for densities to increase with altitude and species composition also changes, the three common species of *Agriotes* declining somewhat on the higher ground.

Roebuck, A. & Broadbent, L. (1945). 'Some notes on *Cryptophypnus quadripustulatus* F. (Col., Elateridae) on grass fields in the Midlands.' Ent. Mon. Mag. 81: 8.

During 1943–4 the wireworms of this species varied in numbers from 17,000 to 400,000 per acre with an average of 105,000 per acre. Distributional and breeding details are given.

Cameron, A. E., McHardy, J. W. & Bennett, A. H. (1944). 'The heather beetle (*Lochmaea suturalis*). An enquiry into its biology and control made on behalf of the British Field Sports Society.' British Field Sports Society, Petworth, Sussex. Pp. 1–69. Price 1*s.*

The adult beetle overwinters and lays its eggs in spring in moist habitats such as *Sphagnum*. Larvae feed on leaves and stems of ling heather during the summer, and adults emerge from the pupae in autumn. Less than 10% of the eggs survive at R.H. 70% and below; consequently dry summers check this pest. The pupae similarly depend upon a high R.H. for successful development. Adults and larvae of the ladybird beetle *Coccinella hieroglyphica* prey upon the larvae of the heather beetle but are probably never sufficiently abundant to effect much control. Drainage appears to be the only way of controlling the outbreaks (which occur at irregular intervals), by creating moisture conditions unfavourable for the beetle and favourable for burning the heather. Summer burning kills the larvae and spring burning, though it does not kill many adults, is also valuable because the young heather which follows is far more resilient after an attack by the beetle.

Solomon, M. E. (1945). 'Tyroglyphid mites in stored products. Methods for the study of population density.' Ann. Appl. Biol. 32: 71–5.

Useful summary of the different methods.

Wimpenny, R. S. (1944). 'Plankton production between the Yorkshire coast and the Dogger Bank, 1933–1939.' J. Mar. Biol. Ass. U.K. 26: 1–6.

A series of vertical hauls at a line of six stations 12 miles apart, from Flamborough Head to south-west Dogger Bank, was made every month. Spring maxima of phyto- and zoo-plankton occurred, frequently followed by secondary maxima later in the year. Fat percentages were higher in the first few months of the year. The difficulty of obtaining an absolute measure of phytoplankton production is discussed.

Ellenby, C. (1944). 'Influence of earthworms on larval emergence in the potato-root eelworm, *Heterodera rostochiensis* Wollenweber.' Ann. Appl. Biol. 31: 332–9.

Experiments showed that earthworms influenced (*a*) the number of larvae emerging per cyst; (*b*) the rate of emergence; (*c*) the number of cysts producing worms; and (*d*) that the number of emerging larvae per cyst increased with the number of earthworms.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Benson, R. B. (1945). 'Water-shrews in Tring town.' Trans. Herts. Nat. Hist. Fld Cl. 22: 108.

Three records of *Neomys fodiens* far from water, one being caught in a break-back trap in a loft.

Bannerman, D. A. (1945). 'Further notes on chaffinch migration in North Devon.' Brit. Birds, 38: 302–6.

Continuous observation in autumn showed a strong southward movement arriving in north Devon from the north, and (presumably) going overland southwards to the Continent. On some days a clear movement was also noted going north, and it is suggested that these may have been Continental birds going to Ireland for the winter (marking has shown that this occurs).

Dannreuther, T. (1945). 'Migration records, 1944.' Entomologist, 78: 49–56.

Includes a general summary of immigrant insect records for 1944, notes on distribution and movements of immigrant species, crude totals of immigrant insects recorded on schedules, recorded abundance and range of regular immigrants, records of vagrant insects, and migration notes from abroad.

Pierson, L. G. (1945). 'The return of *Pararge aegeria*.' Entomologist, 78: 29.

The speckled wood butterfly was common in the Marlborough College district 1864–81; in 1882 and 1883 it decreased rapidly in numbers and then vanished. Single specimens were taken in 1895, 1896, 1908, 1916 and 1922. Recent records are 1939, two specimens; 1942, one specimen; 1943, four specimens. In 1944 it seems to be locally not uncommon. *P. megera* (wall butterfly) was common up to about 1901, then it decreased. Between 1906 and 1915 only one specimen was taken. From 1916 onwards the return was rapid and it is now common again.

Harrison, J. W. Heslop (1945). 'The peacock butterfly (*Nymphalis io* L.) reaches the Isle of Rhum.' Entomologist, 78: 46.

This butterfly reached Rhum in September 1943 and reappeared in the spring of 1944. It was observed in Raasay 8 years ago, the difference no doubt being due to the easier access from the mainland.

Harrison, J. W. Heslop (1945). 'The comma butterfly (*Polygonia c-album* L.) in Cumberland.' Entomologist, 78: 47.

This butterfly is still extending its range and has now reached Murrayholme, just north of Bewcastle.

Crisp, E. (1945). '*Papilio machaon* in East Sussex.' Entomologist, 78: 26.

Two larvae of the swallow-tail butterfly were found on carrot in a garden. N. D. Riley adds an editorial comment that all the *P. machaon* taken in Kent and Sussex of recent years that he has seen are of the Continental race, not the indigenous English race.

Dannreuther, T. (1945). 'Moths at a searchlight.' Hastings Nat. 6: 153–7.

Collections made at St Leonards-on-Sea gave a number of migrant species, particularly *Plusia gamma*, *Amathes c-nigrum* and *Herse convolvuli*, in July and August.

de Worms, C. G. M. (1945). 'Further occurrence of *Hyloicus pinastri* in Salisbury.' Entomologist, 78: 13.

The pine hawk moth is well established in the Salisbury district and is apparently spreading rapidly through the southern counties.

Buckstone, A. A. W. (1945). 'Increase of *Sphinx ligustri* in East Surrey.' Entomologist, 78: 13.

During the past four years there has been a progressive increase in numbers of the privet hawk moth in East Surrey.

Lees, F. E. (1945). 'The striped hawk moth invasion of 1943.' Trans. Torquay Nat. Hist. Soc. 9: 67–72.

Observations on the larval behaviour and colouring of *Celerio livornica* bred from eggs obtained from females of the 1943 invasion. The species is very sensitive to cold which prolongs the period between moults considerably.

Jary, S. G. & Rolfe, S. W. (1945). 'The leek moth.' J. Minist. Agric. 52: 35–7.

The caterpillars of this European moth, *Acrolepia assectella*, which attack leeks, onions, shallots and garlic, appeared in the coastal areas of Sussex, Kent and East Hampshire in 1943 and in the Isle of Wight in 1944 presumably as the result of immigrations.

Fraser, F. C. (1945). '*Sympetrum flaveolum* (L.) (Odon., Libellulidae) in Bournemouth.' Ent. Mon. Mag. 81: 47.

Records this immigrant dragonfly from Wither Moor (Dorset) near Bournemouth and Robin Hood's Bay, north-east Yorks.

Verdcourt, B. (1945). 'Observations on the fauna of static water tanks.' Ent. Mon. Mag. 81: 141.

Thousands of nymphs of a species of the bug *Notonecta* observed in a water tank in London. Sporadic observations on a small tank in Luton showed the following succession: algae, a relatively large water beetle, *Ilybius fuliginosus* which left almost immediately, *Culex pipiens* ovipositing, larvae of this species, *Ilybius fuliginosus*. A month later *Gerris lacustris*, *Sigara lateralis* and nymphs of both seen. A year later *Notonecta* nymphs and *Gyrinus substriatus*.

Massee, A. M. (1945). 'Occurrence of *Elatophilus nigricornis* (Zett.) (Hem., Anthocoridae) in Hampshire and Kent.' Ent. Mon. Mag. 81: 47.

The headquarters of this insect seem to be in Scotland, but it has now been noted in four English counties and its distribution appears to be extending southwards.

Falconer, D. S. (1945). 'On the behaviour of wireworms of the genus *Agriotes* Esch. (Coleoptera, Elateridae) in relation to temperature.' J. Exp. Biol. 21: 17–32.

Soil temperatures in Britain are seldom sufficiently extreme to kill. Between 8 and 25°C. the speed of crawling increases linearly and burrowing activity is greater at higher temperatures. After a sudden fall of temperature from 16 to 6°C. the rate of burrowing was higher at first than later.

Falconer, D. S. (1945). 'On the movement of wireworms of the genus *Agriotes* Esch. (Coleoptera, Elateridae) on the surface of the soil and their sensitivity to light.' J. Exp. Biol. 21: 33–8.

Wireworms deprived of food travelled on the surface of the sand, random movements bringing them up except when the air was not of sufficient humidity. Despite their very strong negative reaction to light, hungry wireworms emerged and crawled about for some time under artificial light.

Parker, H. J. (1945). 'Massing of ladybirds: a further note.' Entomologist, 78: 43.

Large numbers of *Coccinella septempunctata* found on sea-front at Brighton, Sussex, 4 August 1944. The massing of ladybirds seems to have extended along the coast from Essex to St Leonards-on-Sea.

Hinton, H. E. (1945). 'The species of *Anthrenus* that have been found in Britain, with a description of a recently introduced species (Coleoptera, Dermestidae).' Entomologist, 78: 6–9.

A. verbasci, *A. musaeorum* and *A. fuscus* are common and widely distributed in the British Isles. *A. pimpinellae* and *A. scrophulariae* are occasionally found in Britain, particularly in collections of dried insects, but it appears that neither are well established. *A. vorax* was recently added to the list of introductions and *A. coloratus* is here recorded for the first time. A key for identification of adults is given.

Moreton, B. D. (1945). 'On the migration of flea beetles (*Phyllotreta* spp.) (Col., Chrysomelidae) attacking *Brassica* crops.' Ent. Mon. Mag. 81: 59–60.

Invasion of newly germinated crops was negligible in dull weather. In sunny but windy weather it was slow, the beetles entering from the neighbouring established and infested crops or from hibernation quarters by short flights. Under sunny conditions with breeze (force 2) whole crops became heavily infested in one or two days. Migration was a random dispersal under suitable weather conditions rather than attraction from a distance by *Brassica* plants. Knowledge of influence of weather conditions on movements of flea beetles is essential in timing application of insecticides.

Freeman, R. B. (1945). 'Note on colonization by fleas.' Ent. Mon. Mag. 81: 38.

Samples of wheat from a box used as a feeding point for brown rats (*Rattus norvegicus*) were examined daily for fleas. Examination was made to see that no fleas remained in the box and fresh wheat was supplied daily. The number of rats visiting the bait box was not more than 15, but in 17 days 298 (186 ♀♀, 113 ♂♂) fleas (*Nosopsyllus fasciatus*) were brought in so that each rat averaged 19·9 fleas. Larvae appeared on five occasions indicating that the fleas were setting up a new breeding point. Statistical examination of the sex ratio showed that the sexes were not equal in the population.

Petherbridge, F. R. & Jones, F. G. W. (1944). 'Beet eelworm (*Heterodera schachtii* Schm.) in East Anglia, 1934–43.' Ann. Appl. Biol. 31: 320–32.

Distribution indicates that it is not indigenous unless it was originally confined to a few small inaccessible localities. The establishment of the beet-sugar industry has increased the rate of spread which is still in the early stages.

7. REPORTS OF ORGANIZATIONS

Lancashire and Cheshire Fauna Committee (1945). 'Twenty-sixth Report and Report of the Recorders for 1939–42. Part II.' Pp. 39–74. ['Report on the mammals, reptiles and amphibians, 1939–42', by R. K. Perry.]

Distribution and ecological records of mammals, reptiles and Amphibia (by R. K. Perry), and of birds (by A. W. Boyd). The sand lizard (*Lacerta agilis*), common lizard (*L. vivipara*) and natterjack toad (*Bufo calamita*) are still common on the Formby-Ainsdale sand dunes, the last occurring also on the Wirral coast of Cheshire. Apart from numerous local records of birds, there are fuller ecological notes on the goldfinch (*Carduelis carduelis*), stock dove (*Columba oenas*), sand-martin (*Riparia riparia*), teal (*Querquedule crecca*) and curlew (*Numenius arquata*).

British Trust for Ornithology (1944). Tenth Report. 14 pp.

A short war-time report, indicating progress in various field inquiries: the hatching and fledging inquiry, which is accumulating data on clutch size and egg and chick mortality, has reached a stage where analysis of records for some species, e.g. blackbird, can begin.

British Trust for Ornithology (1945). Eleventh Report. 18 pp.

Summaries of investigations still going on show that economic work on wood-pigeons has now reached the stage of being written up for publication. Mortality in this species during the war has been high, due to the market value of the adults and to the abundance of nest predators. The fulmar inquiry has shown that the species has started now to nest in Cornwall and that casual birds are found all along the south coast.

Hutton, J. A. (1945). 'Wye Salmon, 1944: Report of the Wye Board of Conservators.' Salm. Trout Mag. Lond. No. 114: 162–75.

The total catch of salmon on the Wye was one of the smallest of the century (2596 fish weighing 33,297 lb.). This was due to abnormal weather which reduced the rod catch and to the failure of the run of large (3 years sea life and upward) fish. Comparative data for previous years are included.

Yorkshire Fishery District (1944). Seventy-Eighth Annual Report on the Salmon, Trout and Freshwater Fisheries in Yorkshire (by **R. W. Ward**). 28 pp.

The total catch of salmon was 120 fish weighing 1763 lb. and of migratory trout 1958 weighing 8030 lb. The catch of brown trout by anglers is described as 'fair' and of other freshwater fish (roach, dace, chub, barbel and grayling) as 'good'. Comparisons are made with previous years.